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OBSERVATIONS ON THE BIOLOGY AND LARVAE OF THE ANTHOMYIDAE

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(With 157 Figures in the Text)

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INTRODUCTION

THE study of the larvae and biology of the Anthomyidae has formed the subject of several important researches and as a result a great deal of information on different aspects of this subject has accumulated.

It is to Portchinsky (1910) that we owe the first comparative study of the coprophagous anthomyid larvae and of the life histories and activities of the carnivorous types living in the same medium. While Portchinsky was concerned mainly with the habits and metamorphoses, Keilin (1917) gave us a more complete account of the structure of a large number of carnivorous larvae frequenting widely different environments. Keilin, moreover, discovered and emphasized the importance of that characteristic structure, the buccopharyngeal or cephalopharyngeal skeleton, and has shown the remarkably close relation between the form of this skeleton and the habits of the larvae. In that paper, Keilin, discussing the characters of saprophagous

anthomyid larvae, says that, "unfortunately our knowledge of the latter is very fragmentary and incomplete and it is actually impossible for us to have a more or less general idea of these larvae". Since these words were written there has been very little additional information on the subject, and it is one of the objects of this present paper to contribute some material towards the filling up of this obvious gap in our knowledge.

For several years I have had unusual opportunities for investigating the biology of these anthomyids which spend the larval stage in cow-dung. During that time I have accumulated sufficient material to describe not only the habits and activities of the adult flies through the year, but also to describe in some detail the course of development and the morphology of the larvae in all their stages. Of these dung-frequenting anthomyid larvae five species are purely saprophagous and coprophagous, feeding entirely on the dung. These are: *Cryptolucilia cornicina* F., *Dasyphora cyanella* Mgn., *Haematobia stimulans* Mgn., *Morellia simplex* Loew. and *Hylemyia variata* Fallen. Certain aspects of the biology and larval structure of *Stomoxys* and *Musca* have been discussed, since, although they are not members of the cow-dung community, their larvae are purely coprophagous, living in artificial accumulations of animal faeces and other waste matter. Two species, *Mesembrina meridiana* L. and *Polietes hirticrura* Meade, have larvae which may feed on dung alone but which may, if the opportunity arises, become carnivorous, preying on other larvae in the community. These larvae have been called semi-carnivorous and they might equally well be described as potential or facultative carnivores. To this same community belong four species whose larvae in the 3rd stage live a completely carnivorous existence, feeding entirely on other living larvae. These have been called carnivorous forms, but in order to emphasize the fact that living food is absolutely necessary for their existence they might be more suitably described as obligative carnivores in distinction to the facultative carnivores described above. These four species are: *Myiospila meditabunda* F., *Mydaea urbana* Mgn., *Hebecnema umbratica* Mgn. and *Mydaea pagana* Fabr.

The life histories of many of these species have been followed in whole or in part by Portchinsky (1910), but his descriptions and figures of the highly important buccopharyngeal armature are incomplete and inadequate. His important work unfortunately is written in Russian, and the only results of his extensive observations which I have been able to appreciate and compare with my own are the brief summaries and abstracts in the writings of Keilin.

These above-mentioned anthomyids, which in the adult state frequently have widely different habits and distribution, become in the larval stage members of a very compact and complete little ecological community whose activities are restricted to a single cow-dung dropping or dung-cake.

In order to emphasize the fact that these different species are closely related systematically, and that their activities, in the larval state at least, are intimately bound up with each other and are carried out under precisely

similar environmental conditions, I have paid special attention to three aspects of their biology:

(1) A comparison of the ovipositing habits and eggs of the females.

(2) The development and structure of the larvae in relation to habit, i.e. whether they are coprophagous, semi-carnivorous, or carnivorous.

(3) The development and structure of the larvae in relation to the systematic position of the adults.

I have also described the biology of two anthomyids outside the dung community. These are *Muscina pabulorum* Fallen which is semi-carnivorous, and *Phaonia variegata* Mgn. which is carnivorous in the larval state.

Since I have had to deal with such a large amount of new and undescribed material I have found it impracticable to spend time in describing the complete structure of even a single larva. I have therefore confined my descriptions to the external morphology and to the structure of the buccopharyngeal armature or cephalopharyngeal skeleton. The importance of this skeleton can hardly be over-emphasized, because, not only do the form and arrangement of its component parts serve as an indication of larval habits, as Keilin has shown, but in a great many cases these characters are of specific or diagnostic value, forming a reliable means of distinguishing otherwise very similar larvae. I have also paid attention to the duration of the different stages and larval stadia, but it must be borne in mind that all these observations were carried out in Ayrshire and Arran in the west of Scotland and therefore these figures refer only to that area, and will possibly be found to differ in other parts of the country. Considered in relation to each other, however, these figures should be of more general application.

METHODS

In order to make out the details of the buccopharyngeal skeleton the following method of treatment was found to give the most satisfactory results. The larva is macerated in cold 5 per cent caustic potash for several days, the exact length of time depending on its size. After a few days the anal plate is found to become partly or completely detached. A very fine pipette is introduced into the opening formed, and by means of a rubber connecting tube to the observer's mouth, the soft internal structures of the larva are removed by alternate sucking and blowing, the process being controlled under the binocular microscope. By means of this suction method the larva is thoroughly cleaned, then passed through graded alcohols and finally preserved in clove oil. Storage in clove oil has two advantages. Firstly, the complicated relations between the parts of the skeleton are frequently only clear after a fairly long period in this reagent. Secondly, specimens stored in this way, as opposed to those which are permanently mounted, can always be referred to for re-examination, and can be orientated freely in order to give a complete stereoscopic conception of the skeleton.

Cryptolucilia[1] **(Euphoria) cornicina** F.

This metallic green anthomyid is the most common and conspicuous member of the cow-dung community from the beginning of June till the beginning of September. It may appear as early as the middle of April, and during the next month it gradually replaces *Scatophaga* which is the dominant dung-fly of early summer. *Cryptolucilia* is most abundant during August when one dung-cake may have as many as thirty of these flies, though the number is usually much less than this. During September it is gradually replaced by *Scatophaga* and to a less extent by *Polietes lardaria* Fallen and is seldom seen after the end of that month. The normal colour of this fly, light metallic green, is subject to variation, and I have seen on the same dung-cake, normal flies, dull green flies, coppery coloured flies, and some with metallic copper thorax and green abdomen.

Farmers often point out these flies on cow-droppings as the cause of sheep-maggot, mistaking them very naturally for the similarly coloured Calliphorine *Lucilia*.

Oviposition. The eggs are laid in batches or clusters just under the surface of the dung-cake. There seems to be no special preference for freshly dropped dung, although in dry weather the dung ceases to be attractive after about 2 days. The number of eggs laid in one batch varies a great deal and, while it is usually about thirty, as many as fifty may be laid. The eggs are arranged close together standing vertically in a space hollowed out by the ovipositor of the female. In warm weather large numbers of eggs can be obtained by carefully removing the surface skin from a 2 days' old dung-cake.

The egg (Fig. 145) is very like that of *Musca* but larger, being nearly 2 mm. long, with two faint parallel ribs on the slightly concave dorsal surface. In very warm weather eggs have been observed to hatch in less than 24 hours, but under less favourable conditions they may take 3 days to hatch.

The newly hatched larva is in the 1st instar.

1st stage larva

This larva, as in the case of all other anthomyid larvae, consists of a head segment, three thoracic segments and eight abdominal segments. It is metapneustic with the posterior spiracles protruding from the posterior face of the last abdominal segment (Fig. 5). On the ventral surface of the anterior borders of abdominal segments II–VII are broad double belts of spines extending about half-way up each side of the segment. There are also very faint bands of spines on the front borders of the 3rd thoracic and 1st abdominal segments. The anal, or perianal, plate (Fig. 5, *a.pl.*), as in most 1st stage anthomyid larvae examined, is distinct and extends more than half-way up each side of the last abdominal segment.

Buccopharyngeal armature (Fig. 4). This is of typical 1st stage construction.

[1] *Pseudopyrellia* Girschner.

The delicate pharyngeal sclerite or basal piece (*B.*) has slender, pointed, backwardly projecting dorsal and ventral cornua. The anterior dorsal bridge (*d.b.*) is well developed and forms a complete arch.

The long, slender, forward prolongations of the basal piece embrace distally the 1st stage hypostomal sclerite or intermediate piece (*m.*). Anterior to this is the median dorsal sclerite (*m.d.s.*) which is considered to be homologous with the labrum, and below this are the paired *t*-pieces (*t.sc.*) homologous with the labium (Keilin, 1915). The head bears paired antennae (*ant.*) and maxillary palps (*mx.p.*). Larvae were found to complete the 1st stage, and to attain the 2nd stage about 18 hours after hatching, being then 4 mm. long

2nd stage larva

This larva is amphipneustic with 7-lobed anterior spiracles on the 1st thoracic segment, and each of the posterior spiracles has two sinuous slits.

Buccopharyngeal armature (Fig. 12). This is very different from that of the 1st stage larva. The basal piece (*B.*) is large and well developed and has a reticular dorsal bridge (*d.b.*). The forward projecting arms are further connected by a strong transverse ventral bar. In front of the intermediate piece (*M.*) is a pair of peculiar angular sclerites (*an.s.*) of doubtful homology which occur in many other 2nd stage anthomyid larvae. The lateral hooks or crotchets (*l.h.*) are short, weakly developed and closely apposed. Lying ventral to these is a pair of distinct sclerites (*l.sc.*) which probably correspond to the semicylindrical chitinized structures of the 2nd stage larva of *Ophyra leucostoma* Weid. described by Keilin & Tate (1930), which approximate to form a funnel-like entrance to the oral aperture. Since these sclerites occur in many other 2nd stage anthomyid larvae, and since together they often form a kind of spout or lip, I propose to call them the labiate sclerites. At an average daily dung temperature of 18° C. larvae attained the 3rd stage about 48 hours after hatching, but at an average temperature of 15° C. larvae at this time were still in the 2nd instar.

3rd stage larva

The 3rd stage larva is also amphipneustic. The anterior spiracles have 7 lobes on each side; the posterior spiracles (Fig. 154) have three sinuous slits which are folded in almost exactly the same way as those of Musca. In the mature larva the spiracular plates are closely apposed and heavily chitinized, so that the peritreme and external scar, with its small central aperture, are not so distinct as in Musca. The slits are very distinct and have a ladder-like appearance due to regular transverse bars. Round the periphery are the faint openings of perispiracular glands. Double spine pads are present on the front borders of abdominal segments II–VII, and the last abdominal segment bears a distinct anal plate (Fig. 11). On the ventral surface of the last abdominal segment, just behind the anal plate, are three prominent anal papillae projecting downwards and backwards.

The larvae of *Cryptolucilia* are said to be distinguished by their brilliant blue colour (Howard, 1900). I have found this to be a very variable and unreliable character. Mature larvae collected from dung-cakes in the field have a definite shimmering bluish colour, more intense in some aspects than in others, and often a slight evanescent tinge of green and bronze. Just before pupation the semi-transparent larva becomes white and opaque with no suggestion of blue. Larvae bred in artificial cultures never possess any bluish colour, but appear whitish or creamy throughout the whole larval period. Moreover, they never grow as large as they do under natural conditions in the field, and it seems probable that the colour may be related to a constant and plentiful supply of soft moist dung, and to other environmental conditions which are of necessity lacking in cultures.

Buccopharyngeal armature (Figs. 1, 2). The basal piece (*B.*) is strongly chitinized and deeply excavate posteriorly. The anterior dorsal bridge is reticulate (*d.b.*) and complete, and in dorsal view (Fig. 2) is seen to have two forwardly projecting lobes and a bifid median process extending backwards. The lightly chitinized ventral part of the basal piece has a series of longitudinal pharyngeal ridges. The anterior arms of the basal piece are prominent and connected by a transverse ventral bar. Articulating with these is the intermediate piece (*M.*) which is massive and of typical H-shape. It receives ventrally the termination of the common salivary duct.

The lateral hooks (*l.h.*) are closely apposed and each has a broad basal part tapering gradually in a curve to a point. Articulating with the basal part of the lateral hooks is a pair of triangular dental sclerites (*d.sc.*) which are separate and do not form a true median ventral arch. In front of these is a pair of very small accessory sclerites (*a.sc.*). The head bears conspicuous antennae (*ant.*) and maxillary palps (*mx.p.*).

Cryptolucilia is a purely saprophagous and coprophagous larva, and thrives on a diet of pure cow-dung. Considering the large number of eggs which are laid on a single dung-cake in warm weather, these larvae are probably the most generally dominant inhabitants of cow-dung, and not only do they play an important part in the eventual consumption and disintegration of the dung-cake, but they also, as will be considered in more detail later, form the principal basic food of all dung-frequenting carnivorous larvae.

At the beginning of the 3rd stage the larvae are 7–8 mm. long, and by the time they are ready to pupate they are 13 mm. long.

Puparium (Fig. 52)

The puparium is of the ordinary *Musca* type, and is light brown, 6–7 mm. long and smoothly barrel shaped. On the last abdominal segment, the posterior spiracles of the 3rd stage larva are still prominent, and ventrally the now heavily chitinized anal plate is a conspicuous feature.

The prothoracic nymphal spiracles (Fig. 53) project dorso-laterally just in front of the boundary between the 1st and 2nd abdominal segments.

On emergence of the imago, the puparium opens by a circular split round the 1st abdominal segment, just in front of the pupal spiracles, and by a transverse semicircular split extending forwards from this round the front end of the puparium. Of the two caps thus formed, the dorsal one bearing the anterior spiracles of the 3rd stage larva usually separates off, while the ventral one bearing the buccopharyngeal armature usually remains attached. The pupal period normally lasts about 3 weeks, but during a warm July the complete life cycle was passed in 22 days.

Dasyphora cyanella Mgn.

The only record of observations on the life history of this species which I can find is that of Banks (1912) who, quoting Portchinsky (1910), says that while *Dasyphora pratorum* is viviparous, *D. lasiophthalma* (synonymous with *D. cyanella*) is oviparous, laying its egg in cow-dung. There seems to be some confusion about the synonymy of this species; not only has it been referred to under the specific names of *lasiophthalma* and *eriophthalma* but also it has frequently been ascribed to the closely related, but distinct, genus *Pyrellia*. This latter genus however seems to be unrepresented in the area in which I have worked, and I find that all those flies which were caught in many different places at various times of the year, and which I originally considered to be species of *Pyrellia*, really belong to the genus *Dasyphora*. I am indebted to Mr J. Smart of the British Museum for first pointing out the correct identity of this fly.

Dasyphora resembles *Pollenia* and differs from most other anthomyids in that it normally passes the winter in a hibernating adult stage. It may occur outside as late as the middle of November, but after that time it can only be found inside outhouses and dwelling houses.

The adults hibernate in nooks and crannies, behind pictures, under stair carpets, in curtains and round the cornices of rooms. At any time during the winter months they will appear from these hiding places if the room is heated well above its normal temperature. The general laboratory at the Marine Station at Millport is heated for the first time each year when the spring class of students assembles there at the end of March and during that week *Dasyphora* as well as *Pollenia rudis* may frequently be seen crawling inside the windows.

The flies usually appear outside about the first or second week of April, but I have seen them on laurel bushes as early as the second week of March and on exactly the same day as *Pollenia* was first seen out of doors that year. The behaviour of these two flies during the winter is strikingly similar and they are equally capable of surviving considerable degrees of coldness in unheated rooms or outhouses. During the summer, from the end of May onwards, females may be seen ovipositing on cow-dung in the fields, but at no time are they common, and it is only very occasionally that two females are seen

ovipositing on the same dung-cake. The eggs are laid in a manner very similar to that of *Cryptolucilia* in batches of 25–30 just under the surface of the dung.

The egg (Fig. 144) is very like that of *Cryptolucilia* but is slightly longer, over 2 mm. in length, and more slender. A pair of parallel rib-like thickenings run nearly the whole length of the slightly concave dorsal surface and they show the same degree of development as in the egg of *Musca* or *Cryptolucilia*. Although eggs may take 2 or 3 days to hatch, I have found that in very warm weather the larvae may emerge 24–30 hours after the eggs are laid. On hatching the egg opens by a long split just lateral to the dorsal strip; occasionally it may open by two splits so that the dorsal strip becomes free except at the posterior end.

1*st stage larva*

The newly hatched larva is in the 1st stage and is metapneustic. The posterior spiracles (Fig. 9, *p.sp.*) project as paired openings from the posterior face of the last abdominal segment. Well-developed ventral bands of spines (Fig. 6) are present on the anterior borders of abdominal segments II–VII, while weakly developed spine bands occur on the anterior borders of abdominal segments I and VIII. On the ventral surface of the last abdominal segment is a distinct anal plate like that of *Cryptolucilia*. The head (Fig. 7) bears paired antennae (*ant.*) and maxillary palps (*mx.p.*).

Buccopharyngeal armature (Fig. 7). The form and relation of the different parts of the skeleton are very similar to that of the 1st stage *Cryptolucilia* larva. The basal piece (*B.*) has slender backwardly directed cornua and a well-developed anterior dorsal bridge (*d.b.*). As in *Cryptolucilia* the basal piece extends forwards as a pair of slender processes which articulate with the delicate middle piece (*m.*). On the roof of the buccal cavity is the median dorsal sclerite (*m.d.s.*) and below this the paired *t*-pieces (*t.sc.*). At normal summer temperatures the 1st stadium was found to last about 25 hours although a few of the larvae had not reached the 2nd stage by this time.

2*nd stage larva*

The 2nd stage larva is amphipneustic. The prothoracic spiracles are 7-lobed and each of the posterior spiracles has two slits. Ventral spine pads are present on the front borders of abdominal segments I–VII.

Buccopharyngeal armature (Fig. 24). There is also a close resemblance between the skeleton of the 2nd stage and that of the corresponding stage of *Cryptolucilia*. The basal piece (*B.*) is large and well developed and has a prominent reticulate dorsal bridge (*d.b.*). The anterior arms are connected by a transverse ventral bar as in *Cryptolucilia*. The middle piece (*M.*) and the closely apposed lateral hooks (*l.h.*) are also very like those of *Cryptolucilia*, as also are the sclerites of doubtful homology which I have called the angular sclerites (*an.s.*) and the labiate sclerites (*l.sc.*). At an average temperature of

22° C. the 2nd stadium lasted about 30 hours, the young larvae at this stage being 7–8 mm. long.

3rd stage larva

The larva at this stage is amphipneustic and the anterior spiracles (Fig. 8) have 7 lobes. The posterior spiracles (Fig. 155) on the posterior face of the last abdominal segment have three sinuous slits on each side. The spiracular plates of the mature larva are slightly more separated than in *Cryptolucilia* and are even more heavily chitinized so that the small central aperture of the external scar is in most cases obscured. The peritreme is indistinct and the four openings of the perispiracular glands are very small. The most distinctive feature of the spiracles, however, and one that distinguishes them from those of *Musca* and *Cryptolucilia*, is that the middle spiracular slit on each side is folded in exactly the opposite way from those larvae. The dorsal part of this slit is directed towards the external scar and the ventral end towards the peritreme, while in *Musca* and *Cryptolucilia* the reverse is the case. The ventral spine pads are well developed on abdominal segments II–VII, corresponding to the six prominent spine bands of the 1st stage larva.

On the ventral surface of the last abdominal segment is a distinct anal plate (Fig. 10) convex anteriorly and concave posteriorly. Behind this plate, at the posterior limit of the ventral surface of the last abdominal segment, there are, as in *Cryptolucilia*, three prominent post anal lobes (*p.a.l.*).

The head (Fig. 3) is slightly bilobed in front and bears paired antennae (*ant.*) and maxillary palps (*mx.p.*). At no stage have the larvae of *Dasyphora* any trace of bluish colour, but are always whitish or creamy and opaque.

Buccopharyngeal armature (Fig. 3). This skeleton is interesting when compared with that of the closely related *Cryptolucilia* (Fig. 1), because, although there is a general resemblance in relation to the very similar modes of life, yet there are minor constant differences which enable the two types to be distinguished easily. The following comparison may also help to illustrate the way in which the characters of the skeleton can be made use of as important diagnostic features. The basal piece (*B.*) is in its hind part like that of *Cryptolucilia*, but in front the dorsal bridge (*d.b.*) is less reticulate and its bifid median process has more widely separated, longer and more slender blades. Just anterior to the dorsal bridge there is on each side a characteristic rounded lobe which is absent from *Cryptolucilia*. The ventral surface of the basal piece has 8 well-marked longitudinal pharyngeal ridges. The middle piece (*M.*) is massive and each arm of the H has a pointed ventral expansion. The lateral hooks (*l.h.*) are like those of *Cryptolucilia* but are longer and less curved. The left hook is sometimes a little shorter than the right hook but this is not a constant character. The median ventral arch is represented by two separate triangular pieces, the dental sclerites (*d.sc.*). The pair of accessory sclerites which in *Cryptolucilia* are feebly developed are here large and distinct (*a.sc.*) and elongate triangular in side view. The larva of *Dasyphora* lives as a pure coprophage in all its stages, thriving on a diet of pure cow-dung. Its develop-

ment seems to be rather slower than that of *Cryptolucilia*, and its whole life cycle may take 8 weeks with a larval period of 4 weeks. The full-grown larva is 14 mm. long.

Puparium (Fig. 48)

The puparium is of the ordinary *Musca* type, about 6·5 mm. long and darker brown than that of *Cryptolucilia*. The rounded posterior end has the 3rd stage spiracles with the spiracular design still visible. The anal plate is not very distinct. The prothoracic nymphal spiracles (Fig. 49) open to the exterior, as very small pupal horns, dorsolaterally just in front of the border between the 1st and 2nd abdominal segments. The splitting of the puparium and the emergence of the imago are precisely similar to that of *Cryptolucilia*. The pupal period in summer was found to last 3–4 weeks.

Haematobia stimulans Mgn.

The general habits of *Haematobia stimulans* are fairly well known but little attention has been paid to the habits and structure of the larva. In the short account of the biology of this fly by Portchinsky (1910) there are no figures showing the buccopharyngeal armature of any of the three larval stages. For a few years I have paid particular attention to the bionomics of this species in South-West Scotland, and to its comparison with the closely related biting fly *Stomoxys*. These two species are the only common blood-sucking Muscinae in this area, but while *Haematobia* is still a wild species, having much in common with other dung-frequenting Anthomyidae, *Stomoxys*, on the other hand, is a more domesticated species which has many characters in common with *Musca domestica*.

The adults of *Haematobia* are commonly seen, during summer months, on cattle in the fields, and their blood-sucking activities seem to be almost entirely restricted to these animals. I have never seen them on horses, and, despite innumerable opportunities, I have never been bitten by them myself. Séguy (1923) says that they often bite human beings, and that it is the female alone which sucks blood; but this has not been my experience. Both males and females, with the latter predominating, occur commonly on the cows, and I have observed closely one case in which a cow was more disturbed by a male fly trying to settle on it than by the numerous females already present. Males and females swollen with blood are frequently seen on wooden gates and palings round fields where cattle are grazing.

In nearly every case flies are seen grouped on that part of the body above the forelegs, they never occur on the head or base of horns, nor are they found on the hind part of the body within reach of the tail. At no time, however, are they so numerous as to cause extreme annoyance, 25 being the greatest number of flies ever seen on a single cow; and in this area, at least, they can only be considered of minor economic importance. *Morellia* causes far more annoyance and irritation. *Haematobia* seems to have no preference for any particular kind of cow; they are sometimes more common on black cows but

this is by no means constant. Ruminating cows which are lying down are usually more troubled by flies since the use of the tail is restricted, and one animal with an abnormally short tail was definitely more pestered than the other members of the herd.

Haematobia occurs on cattle in the fields from the beginning of June until the end of September, and, unless gorged with blood, the flies seem to follow the cattle very closely, never being found in the empty byres during the day. In this they differ from *Stomoxys* which I have never seen following the cattle into the fields and which is very common in the empty byres and on the byre doors in summer. Both these flies are most plentiful in late summer such as the early part of September, *Haematobia* on cattle in the fields and *Stomoxys* in the farmyard and byre.

Before considering the relation between the habits of *Haematobia* and the rather peculiar and varied methods of looking after the cattle throughout the year in Ayrshire, the distinctive features of the oviposition of this fly will be discussed.

The most striking feature of the act of oviposition is its almost complete restriction to fresh newly-dropped dung. The whole process can be followed by watching the freshly dropped dung closely, and it is on a very large number of such observations that the following account is based. The pregnant females begin to appear about 10 sec. after the dung is dropped; and it is an interesting fact that most of them, before they began ovipositing, sucked up some of the liquid dung. This latter habit certainly is an unusual one for a blood-sucking fly. Newstead (1906) observed two specimens of *Stomoxys* settling on fresh cow-dung and feeding on the moisture on it, but he considered that such a phenomenon was exceptional or rarely seen in nature. I myself have seen the male cleg, *Haematopota pulvialis*, engaged in a similar act on fresh cow-dung, but it is doubtful if the habit is shared by the female.

Immediately after sucking the dung, the female *Haematobia* crawls over the dung, protruding and withdrawing its ovipositor, until finally it lays a single egg usually near the edge of the cake and with its tip just visible. This may be repeated as many as five times but not more; many of the females lay only one or two eggs on each cake. If a pregnant female is caught in a small glass tube and kept for a short time in the dark, it lays its full complement of eggs inside the tube, the number being very constant, about 25–29. Swollen pregnant females found on gate-posts and fences are seldom found to contain more than this number of eggs, although one fly was recorded with 44 mature eggs in its abdomen. Fresh dung has a characteristic transient smell which may be the source of attraction for the females. The stimulus to oviposit is very strong and flies prevented from settling on the dung return again and again, but they are not attracted by the opening up or turning over of dung which is only a few hours old. The temperature of fresh dung was found to be 38·5° C. which is approximately that of the body of the cow. It cools slowly and fairly uniformly and 1 hour afterwards it is about 32° C. The eggs therefore

start their development in very favourable conditions and difficulty is often encountered in trying to breed them in dung at ordinary temperatures. It is natural to suppose that, since *Haematobia* leaves the cow in order to oviposit, it will return to the cow after the eggs are laid. This is surprisingly difficult to verify as it is almost impossible to follow the flight of the fly. The flies probably do not return to the same cow since, by the time oviposition is over, that cow may be over a hundred yards away, and other cows nearer at hand would obviously be equally suitable hosts. There is a certain regularity in the times of defaecation of cows; the process does not take place in such a haphazard way as might be imagined. When cows rise up after a long interval of rumination they nearly always defaecate at once, and, since the cattle move about together and collectively behave as a single individual, this means that they all defaecate together within a very short period. This is followed by an interval of grazing which may last an hour or two, and in which defaecation is reduced to a minimum. By moving slowly among a herd of resting cows and disturbing one at a time, a continual supply of fresh dung can be obtained and many observations made and verified. This method was also employed in the study of *Myiospila* and its ovipositing habits.

In summer the cows are out in the fields all day and night except for two milking periods about 6 a.m. and 4 p.m. respectively. In winter, however, different methods are used on different farms; the cows may be kept in the byre at night and let out for a longer or shorter period during the day, depending on weather conditions.

On the other hand the cows may be taken into the byre from the fields about the first week of November, and from then until the beginning of May they are kept there, never being let out once during all that time. Such a byre full of cows was examined early in March on a bright warm spring day. It contained 25 cows which had been kept indoors for 4 months. They were so closely packed that, when two adjacent cows were lying down, there was scarcely room to pass between them. The temperature of the byre was high and the atmosphere very stuffy, so that the conditions were highly unnatural for the cows and correspondingly favourable for the hibernation of blood-sucking and other flies. Nevertheless, a careful search of cows, walls, byre partitions, rafters and freshly dropped dung failed to reveal any signs of *Haematobia* or *Stomoxys*. A few flies may have been present in inaccessible nooks and crannies in the roof, but their complete absence from the other sites is surprising.

Up till the beginning of October, *Haematobia* is still fairly common on cows, but by the end of that month it is no longer seen on them. Cows which were let out for a few hours each day during the winter were carefully looked over, but *Haematobia* was never seen between the beginning of November and the end of April, even on fine warm days. Search in the empty byres met with similar results. Cows kept inside all the winter are let out in the first or second week of May, and it is just about this time that *Haematobia* appears.

The time of first appearance is fairly constant, being 5 May and 10 May in two consecutive years, and on these occasions they are seen on gate-posts and fences and on clothes-poles in the garden, nowhere near the cattle. Later they are also seen on beech trees, and many of them have a distensible ptilinum, a certain sign of recent emergence. These observations suggest that *Haematobia*, like the majority of coprophagous anthomyids, passes the winter in the larval state. The flies appear on cows in the fields about the end of May and oviposition occurs a little later.

The egg of *Haematobia* (Fig. 147) is about 1 mm. long, white in colour with a pitted surface. The two parallel dorsal ribs are more distinct than in the eggs of *Musca* and *Stomoxys* and the dorsal strip is broader than that of *Cryptolucilia*. Eggs hatch in from 43 to 48 hours at normal temperatures and, when the young larvae emerge, the chorion does not collapse as in *Cryptolucilia*, but remains rigid, only the longitudinal split outside one of the ribs indicating that the egg is empty.

1*st stage larva*

The newly hatched larva is in the 1st stage, and is metapneustic, the posterior spiracles projecting as a pair of prominent openings from the posterior face of the last abdominal segment. The young larva is very active, and crawls rapidly over the surface and through the dung of the culture, its elongate, pointed anterior end jerking in and out all the time. The larvae were bred between two watch-glasses and during the entire larval period they showed a preference for the surface of the dung, heedless of bright light. This is probably related to the better oxygen supply at the surface of the dung, since the conditions in the field offer a direct contrast, the surface of the dung-cake drying in a day or two to form a very hard white crust, quite impenetrable by delicate larvae. In these cakes the larvae are found near the bottom next to the well-ventilated space between the dung and the earth. The 1st stage larva has a ventral band of spines on the anterior borders of abdominal segments II–VII. On the head segment (Figs. 15, 16) are the prominent paired antennae (*ant.*) and maxillary palps (*mx.p.*).

The buccopharyngeal armature (Figs. 15, 16) consists of the usual sclerites. The basal piece (*B.*) is better developed than that of most other 1st stage larvae, differing from *Cryptolucilia* and *Musca* in the wider separation between the dorsal cornua and the forwardly projecting anterior dorsal bridge (*d.b.*). The ventral cornua project much farther back than the dorsal cornua. The two long anterior arms of this piece articulate distally with the intermediate piece (*m.*) which in turn has lying in front of it the median dorsal sclerite (*m.d.s.*) and ventrally the paired *t*-pieces (*t.sc.*).

The 1st stage was found to last about 25 hours.

2nd stage larva

The 2nd stage larva is amphipneustic with prominent 6-lobed anterior spiracles and posterior spiracles opening by two slits on each side. Also conspicuous, through the transparent cuticle of the living larva, is the transverse connecting arch between the two main lateral trachea, just behind the anterior spiracles; this is not seen in the 1st stage larva.

The buccopharyngeal armature (Figs. 17, 23) consists of the normal 2nd stage parts, but many of these have become modified in shape and can only be correlated with those of, say, *Cryptolucilia* by means of their corresponding positions. The basal piece (*B.*) is considerably larger and stouter than that of the 1st stage. The anterior dorsal bridge (*d.b.*) is conspicuously reticulate. Connecting the anterior arms of the basal piece is a transverse ventral arched bar like that of *Cryptolucilia*.

The intermediate piece (*M.*) has pointed triangular lateral walls, and has a chitinous prolongation in front which connects it to a short transverse plate made up of two small sclerites.

These paired sclerites (*an.s.*) are probably homologous with the angular sclerites of *Cryptolucilia*, which, though very different in appearance, are situated in a corresponding position. The lateral hooks are very short and closely apposed (*l.h.*) and have lying on each side large pointed pieces (*po.p.*) which probably correspond to the labiate pieces of *Cryptolucilia*. The relations of these sclerites to each other can best be appreciated in a ventral view of the entire skeleton (Fig. 17). In the arrangement of its anterior parts this skeleton differs markedly from most other 2nd stage anthomyid larvae. I have not had the opportunity of examining the 2nd stage larva of *Stomoxys*, and it would be interesting to know if its buccopharyngeal armature is of the usual *Cryptolucilia* type or of this peculiar *Haematobia* type.

Larvae were found to attain the 3rd stage 69–80 hours after hatching and were then about 6 mm. long.

3rd stage larva

One of the characteristic external features of this larva is the attenuation of the anterior segments which gives the body a very long tapering appearance, together with the unusually deep groove between the two prominent diverging lobes of the head. From the mouth opening (Fig. 14) a series of oral grooves (*or.gr.*) radiates out in fan-like fashion over the ventral surface of the head. At the tip of each head lobe is an antenna (*ant.*) and ventral and slightly more medial to this a maxillary palp (*mx.p.*). The larva is amphipneustic and the anterior spiracles, situated laterally about the middle of the 1st thoracic segment, are 7-lobed. The posterior spiracles on the posterior face of the last abdominal segment are widely separated and lie near the dorsal rim of the segment. Each spiracular plate (Fig. 20) is of roughly triangular shape with rounded corners; the three separate slits are very slightly folded, like a laterally compressed **S**, and are arranged more or less in a circle round the

slightly eccentric external scar which has a small vertical central opening. The curvature or degree of folding of the spiracular slits is not obvious, and each slit with the lightly chitinized areas between the folds appears to form a single elongate oval clear space which might easily be mistaken for a spiracular slit of the *Muscina* type. Each spiracular plate is marked with concentric rings of heavy chitinization, giving it a distinctive appearance, and the peritreme is not especially well marked.

If these spiracles are compared with those of the mature 3rd stage larva of *Stomoxys* (Fig. 22) many striking differences and resemblances can be seen between the two. In both species the similar shaped spiracular plates are separated by about twice their breadth, but in *Stomoxys* the **S**-shaped folding of the spiracular clefts is very obvious as compared with that of *Haematobia*, and the slits are distinctly ladder-marked. The spiracular plate of *Stomoxys* is uniformly heavily chitinized and this results not only in throwing the spiracular slits into relief but also in obscuring the limits of the peritreme and external scar. In the centre of the plate is a very small round aperture, and round the periphery are four small openings of perispiracular glands. There are no concentric dark rings like those of *Haematobia*.

Despite these differences the spiracles of *Haematobia* and *Stomoxys* are obviously closely related; they show the same slight degree of folding of the slits which forms a contrast both to the radiating type of *Myiospila* and to the much folded design of *Musca*, *Cryptolucilia*, *Mesembrina*, etc. Furthermore, the spiracular plates are of similar shape and differ from most other related forms in being so well separated.

The ventral spine pads of the *Haematobia* larva are present on the anterior borders of abdominal segments II–VII but form a much less conspicuous feature here than in the 1st stage larva.

The anal plate (Fig. 18) is of the usual shape. The mature larva of *Haematobia* may measure as much as 9 mm. in length and is full grown about 14 days after hatching.

Buccopharyngeal armature (Figs. 13, 14). The armature consists of the same essential sclerites as in the larva of *Cryptolucilia*. The basal piece (*B.*) has a very straight dorsal surface merging into the dorsal bridge (*d.b.*) in front and produced behind into the slender pointed dorsal cornua. The ventral cornua are large and rounded and extend farther back than the dorsal cornua. The ventral surface of the basal piece is marked with longitudinal pharyngeal ridges as in all saprophagous cyclorrhaphous larvae. Uniting the two lateral plates anteriorly is a transverse ventral arch and, in front of this, each plate projects forward to articulate with the middle piece. The middle piece (*M.*) is heavily chitinized and of the usual shape, differing only in detail from that of *Cryptolucilia*, *Dasyphora*, *Morellia*, etc. The lateral hooks (*l.h.*) are of rather unusual shape, each having a strongly bifid base and the left hook being much shorter than the right one. The reduction of the left hook can best be appreciated in a dorsal or ventral view of the armature (Fig. 14, *l.h.*). This latter

condition is a feature common to the 3rd stage larvae of *Haematobia*, *Stomoxys* and *Musca*, and forms a striking contrast to that of *Cryptolucilia*, *Dasyphora*, *Morellia* and many others, in which the lateral hooks are of equal size. The dental sclerites (*d.sc.*) are triangular in shape and, as in all saprophagous anthomyid larvae, they are separate and do not form a median ventral arch.

Puparium (Fig. 54)

The puparium of *Haematobia* is the smallest of all the Muscinae, being only 4·5 mm. long. It is of the normal barrel shape, smooth, circular in section, and light brown in colour.

The last segment bears the prominent, well-separated, posterior spiracles of the 3rd stage larva, and ventrally the now heavily chitinized anal plate. The prothoracic nymphal spiracles (Fig. 55) project laterally just immediately in front of the groove between the 1st and 2nd abdominal segments. On eclosion the puparium opens in a similar manner to that of *Cryptolucilia*. The pupal period was found to last 14 days in July.

Stomoxys calcitrans L.

Stomoxys calcitrans and *Haematobia stimulans* are the only two blood-sucking Muscids which I have found in Ayrshire, and a comparison of their habits and of their larvae reveals at the same time many affinities and many striking differences. Without going into a full account of the biology of *Stomoxys* in this area, I propose to select those parts of its life history which are of special interest when compared with *Haematobia*.

Stomoxys is a domestic fly and is never found at any great distance from farms and country houses. In the farmyard it is one of the most dominant flies in summer, being found outside from the beginning of June until the middle of October. In late summer, especially during September, it occurs in swarms on the byre doors next to the farm midden. Unlike *Haematobia*, it commonly attacks man both out of doors and indoors. They are especially troublesome towards the end of the season and are found inside the house up till the end of November. During the winter months they may be seen occasionally inside the byre, but are not plentiful until April. *Stomoxys* bites cattle in the byre and differs from *Haematobia* in that it never follows the cattle into the fields. I have never seen it on the gates or fences round the fields and it never occurs on either fresh or mature dung-cakes. Despite its common name, *Stomoxys* is not plentiful in stables and is much more partial to byres.

Although much is now known about some aspects of the biology of *Stomoxys*, there is surprisingly little information—in this country at least—about the normal ovipositing habits and natural breeding sites of this fly. Newstead (1906), in his very thorough investigation of *Stomoxys*, only observed the flies ovipositing in the field in a heap of grass mowings, and, although

larvae have been recovered from a great variety of materials, horse manure and stable refuse are usually considered to be the principle breeding sites. My own observations indicate that the ovipositing habits of *Stomoxys* are remarkably constant, and that the type of material selected differs from that usually described.

In late summer, when the flies are most plentiful, females may be seen on the farm dung-heap or midden. This midden contains many different materials such as cow, horse, and pig-dung, and in a few cases human faeces. These materials vary in consistency, from perfectly fresh byre and stable manure which is added every day, to hard caked slabs which have been baked dry by months of exposure to the sun. It is only on these dry, and apparently unattractive, banks of the midden that the females have been seen ovipositing. Fresh cow-dung, horse-dung and pig-dung are equally avoided by the gravid females. Below the hard outer crust, which consists of dried cow-dung together with straw, ashes, and other rubbish, the substance is softer and more moist. Each female lays one or several batches of eggs varying from 5 to 20 in number in the dry cracks and fissures of the crust. A pregnant female was found to contain over 90 mature eggs in its abdomen, which is a considerably greater number than in *Haematobia*. The site of ovipositing was found to be precisely similar in different farmyards, and perhaps the two most striking facts about it are firstly, the dryness and staleness of the material as compared with cow-dung in the field; and secondly, the very high temperature of the midden banks due to the sheltered position in conjunction with complete exposure to the full glare of the sun.

In the 1st stage larva, the buccopharyngeal armature is very like that of *Haematobia*. The basal piece is well developed and shows a similar difference from that of *Musca*, *Morellia*, *Cryptolucilia*, etc., in being elongated so that the anterior dorsal bridge is well separated from the dorsal cornua.

The mature 3rd stage larva may be 12 mm. long and is therefore much larger than that of *Haematobia*. The posterior spiracles have been described along with those of *Haematobia*.

In the buccopharyngeal armature (Fig. 19) the basal piece (*B.*) is of a similar type to that of *Haematobia* but the dorsal and ventral surfaces are more divergent posteriorly, and the anterior arms are heavily chitinized at the tips. The dorsal bridge (*d.b.*) and the anterior arms of the basal piece are more approximated than in *Haematobia*. The intermediate piece (*M.*) is of peculiar shape, a deep posterior excavation on each side dividing it into four backwardly projecting horns. The lateral hooks (*l.h.*), like those of *Haematobia*, are unequal, and the left hook is even more reduced. The dental sclerites (*d.sc.*) are triangular and separate. The larva of *Stomoxys*, like that of *Haematobia*, is saprophagous and coprophagous in all its stages, feeding entirely on dung and similar decaying animal and vegetable substances. In September larvae of *Stomoxys* may be found in nearly every part of the dung-heap except the pure cow-dung. Dung kept porous by being mixed with straw is specially

favoured and the larvae are most common just under the hard crust where the eggs are laid. Here, as well as in horse and pig-manure, the smooth reddish puparia are also found as apparently the larvae do not migrate to drier surroundings prior to pupation.

Morellia simplex Loew.

The species of *Morellia* are among the commonest and most widespread anthomyids. The specific distinctions between the members of this genus are based on male characters alone and these differences are not obvious enough to be appreciated in the field. With regard to the females Séguy (1923) says that, in the absence of constant characters, the females of the four common species cannot be distinguished. In the following account, therefore, I have made no attempt to find out differences, if any, between the habits and larvae of the separate species but have included all observations under the heading of *Morellia simplex*, which is by far the most common species and the only one which has been obtained from the numerous batches of eggs and larvae in this district. Portchinsky (1910) has described the biology of the closely related *M. hortorum* Fallen, but has not given any complete figures of the larval buccopharyngeal armature.

Morellia appears usually about the middle of May and is abundant everywhere, especially on privet and beech hedges, during the summer months, becoming scarce in October. In these various habitats it is frequently accompanied by *Polietes albolineata* Fallen which apart from having a straight 4th longitudinal vein so closely resembles *Morellia* that it is very easy to confuse the two species in the field. *Morellia* has some economic importance because of its habit of settling on horses and cattle, causing intense annoyance and irritation by swarming on the face and round the eyes. This is especially severe in early summer and, as far as cattle are concerned, it is a more troublesome fly than *Haematobia* during June and July. The moist secretion from the eye seems to be the main attraction in most cases. A somewhat similar habit is shown by *Morellia hortensia* Stein. which in Madras sucks the juices exuding from wounds or bites inflicted on cattle by biting flies (Patton & Cragg, 1913).

The ovipositing habits of *Morellia* are very like those of *Cryptolucilia* as the eggs are laid beneath the surface in cow-dung in batches of about 25. The female usually prefers to lay on moist dung in shaded positions, and oviposition is much less common in open exposed fields. Normally there are three or four ovipositing females on the dung 1 hour after it has been dropped. When a cow defaecates the females often suck up some of the semi-liquid dung, and then fly back to the cow again; but occasionally they may oviposit in this interval. In North America *Morellia micans* Macq. breeds almost entirely in human excrement, while in Madras *M. hortensia* Stein. breeds in cow-dung (Patton & Cragg, 1913).

The egg (Fig. 146) is nearly 2 mm. long and almost identical in appearance with that of *Cryptolucilia*. The dorsal ribs are faint and do not project. In

July eggs took 28 hours to hatch at an average temperature of 20° C. In another instance eggs took 36–40 hours to hatch. In every case the newly hatched larvae were in the 1st stage.

1st stage larva

The 1st stage larva is metapneustic. The posterior spiracles (Fig. 30) are heavily chitinized projections from the posterior face of the last abdominal segment and each has a single medial opening; round the rim of this opening is a circle of radiating hairs. Well-marked bands of spines are present on the front borders of abdominal segments I–VII and there is a weakly developed band on the front border of the 3rd thoracic segment. While most strongly developed on the ventral surface these spine bands are almost unique among 1st stage anthomyid larvae in that they are continued up the sides and over the dorsal surface to form a complete ring. The ventral surface of the last abdominal segment bears a distinct anal plate with short bands of spines immediately in front of and behind it. The posterior face of this segment is already at this stage slightly flattened. The head bears paired antennae (Fig. 28, *ant.*) and maxillary palps (*mx.p.*).

The buccopharyngeal armature (Fig. 28) is of the normal *Musca* and *Cryptolucilia* type. The basal piece (*B.*) is delicate with fine pointed, very divergent dorsal and ventral cornua. The anterior dorsal bridge (*d.b.*) is complete and very weakly chitinized. The anterior arms of the basal piece extend forwards to embrace the curved middle piece (*m.*) which in turn has lying in front of it the median dorsal sclerite of typical form (*m.d.s.*). Ventral to this are the curved *t*-pieces (*t.sc.*) homologous with the labium and of the usual shape.

The 1st stage larva is purely coprophagous and very shortly after hatching the coiled gut with its dark brown contents can be seen through the semi-transparent cuticle. Larvae were found to reach the 2nd stage about 18 hours after hatching and at this time were nearly 5 mm. long.

2nd stage larva

The 2nd stage larva is amphipneustic, the prothoracic spiracles being 4–6-lobed and the posterior spiracles (Fig. 44) having two curved spiracular slits on each side. Spines are most strongly developed round the front borders of abdominal segments I–VII. The posterior face of the last abdominal segment is round and flattened and bears a complete ring of spines round its circumference. Spines are also well developed on the ventral surface of this segment.

Buccopharyngeal armature (Fig. 31). The basal piece (*B.*) is rather like that of the 2nd stage *Haematobia*. The dorsal surface is nearly straight and parallel to the ventral surface. The rounded ventral cornua (*v.c.*) are longer than the pointed dorsal cornua (*d.c.*). From the anterior surface arises a large, complete, reticulate or perforate dorsal bridge (*d.b.*). The anterior pointed arms

of the basal piece are connected by a strong transverse ventral bar. The middle piece (*M.*) is H-shaped in dorsal view and the side plates are roughly triangular. Immediately in front of this are the angular pieces (*an.s.*) separated ventrally but closely approximated dorsally and without backwardly projecting processes. The lateral hooks (*l.h.*) are closely apposed and of peculiar shape in that instead of curving down distally towards the mouth-opening they are bent up dorsally and end in a sharp point. The ventral and side walls of the buccal cavity are formed by the labiate sclerites (*l.sc.*) which are united to form a sort of gutter or spout. The head bears paired antennae (*ant.*) and maxillary palps (*mx.p.*); from the groove between the oral lobes fine channels run laterally and dorsally.

I have not noted the exact length of this stadium but larvae examined 42 hours after hatching were still in the 2nd stage, while 8 hours later they were seen to be in the 3rd stage. Without actually observing the ecdysis it is very difficult to tell the difference between a late 2nd stage and an early 3rd stage, since the posterior spiracles in both cases are so heavily chitinized that the slits can hardly be distinguished, and the cuticle is not sufficiently transparent to permit changes in the structure of the armature to be observed.

3rd stage larva (Fig. 25)

The 3rd stage larva is amphipneustic and the anterior spiracles (Fig. 26) have 4–6 lobes.

The posterior spiracles (Figs. 156, 157) are unusual in that the number and arrangement of the spiracular slits in the late 3rd stage are completely obscured by heavy chitinization, and the plates appear as solid black structures each with a slightly raised sculptured external scar. In the early 3rd stage the plates are not quite so heavily chitinized and the very sinuous course of the three spiracular slits can be followed after suitable treatment. The spiracular plates are large and the peritreme is distinct and continuous except at the inner border where it bends in towards the round external scar (*ex.s.*). The spiracular clefts are more folded than in *Cryptolucilia* but less so than in *Mesembrina* and the course of the clefts is quite different from either of these two types.

The external appearance of the 3rd stage larva of *Morellia simplex* is quite distinctive and diagnostic (Fig. 25), and is a feature common to other members of the genus described by Portchinsky (1910) and Patton & Cragg (1913). The cuticle is more heavily chitinized than that of most anthomyid larvae, giving it a brown to dark brown colour, and is broken up into a reticular or honeycomb pattern by a network of ridges (Fig. 34). Complete girdles of spines are present on the front and hind borders of abdominal segments I–VII as well as on the front borders of the three thoracic segments (Figs. 33, 35). The last abdominal segment has its posterior face flattened to such an extent that the larva can be stood up on end quite easily. This face is also broken up by a network of ridges enclosing polygonal areas. The ventral surface of the last segment is

heavily spined and bears an anal plate of rather unusual form (Fig. 27) with a large triangular centre piece and uniformly slender lateral arms.

Buccopharyngeal armature (Fig. 36). The basal piece (*B.*) is of unusual shape; the dorsal and ventral surfaces diverge uniformly from the abrupt front end backwards. The anterior dorsal bridge (*d.b.*) connecting the two lateral plates dorsally is situated farther back than in most other related anthomyid larvae. The dorsal cornua (*d.c.*) are rounded posteriorly and the ventral surface of the basal piece is marked by eight longitudinal pharyngeal ridges. The middle piece (*M.*), which receives the terminal part of the common salivary duct, is short and massive and H-shaped in dorsal view. The lateral hooks (*l.h.*) are of equal size, very slightly curved and have rounded, closely apposed, blunt tips. The feebly developed base of each hook has a large triangular lightly chitinized area. The dental sclerites (*d.sc.*) are triangular and separate, the pointed ventral parts not being connected transversely to form a median arch.

The larva of *Morellia* in all its stages is purely coprophagous, living a sluggish existence in the cow-dung. In relation to its habits the armature is of simple saprophagous type as exemplified by the following selected characters of the component parts. The basal piece with its diverging surfaces, ventral pharyngeal ridges and absence of uniformly heavy chitinization is of true saprophagous type. The loose articulation between the basal piece and the middle piece as well as the wide separation between the latter and the bases of the hooks is another saprophagous feature. The weak development of the lateral hooks, their small degree of curvature and their blunt points are features never found in carnivorous larvae. Finally, the absence of accessory buccal sclerites, together with the presence of distinctly separate dental sclerites, would indicate a coprophagous or saprophagous mode of life.

Morellia has become more specialized than the coprophagous larvae of *Cryptolucilia*, *Dasyphora*, *Musca*, etc., in that while these latter types have no means of protection against the attacks of carnivorous larvae, such as *Myiospila* and *Mydoea*, *Morellia* has developed such a tough cuticle that it is unharmed by these carnivores. In view of this valuable larval adaptation it is not surprising that the species is so abundant and successful in the adult stage.

This larva is also interesting from a systematic point of view since it seems to occupy a unique position. The many peculiar characters which serve to separate it from other anthomyid larvae bear no relation to the systematic position of the adult fly. In no single feature described does the larva resemble those of its nearest relations, *Myiosphila*, *Graphomyia* and *Muscina*. As is so often the case among anthomyid larvae, the structural features are more closely related to larval habit than to systematic position.

Although adult flies may emerge as late as the middle of October, the autumn and winter are usually spent in the larval stage. Larvae found in cow-dung in January produced adults which emerged in the first week of May.

Puparium (Fig. 50)

The form of the puparium is almost exactly like that of the late 3rd stage larva, the only obvious difference being the increased rigidity of the cuticle. The full-grown larva moreover does not leave the cake or move down to ground level but pupates in the dung just as it lies. An unusual feature of the puparium is that the prothoracic nymphal spiracles (Fig. 51) never form a communication with the exterior by means of pupal horns or pupal spiracles. No indication of external pupal horns could be found in puparia either before or after eclosion. The intra-pupal spiracles (*in.p.s.*), on the other hand, are very well developed with numerous stigmatic papillae arranged in a rough pattern and with an additional strongly developed supporting chitinous ring. The absence of the normal communication with the exterior may possibly be related to the peculiar nature of the cuticle which might be slightly porous, allowing a slow exchange of gases to take place between the external atmosphere and the interior of the puparium. The pupal period was found to last 17–18 days in summer and the mode of eclosion is similar to that of *Haematobia* and *Cryptolucilia*.

Hylemyia variata Fallen

(with notes on *Hylemyia strigosa* F.)

The viviparous habits of these and other species of *Hylemyia* are described by Keilin (1916) who also gives a summary of Portchinsky's observations. According to the latter author *H. variata* is either viviparous or larviparous, only laying a single larva, or an egg which hatches immediately after deposition.

The closely related *H. strigosa* has rather similar habits. It is viviparous and the larva which is completely formed under the chorion of the egg often shows superimposed characters of two stages (Keilin, 1915). The 3rd stage larva lives in excrement (Bouché, 1834; Keilin, 1915).

These two species are not very common in the locality in which I have studied them and I have only been able to observe the actual birth of the larva in the field on five separate occasions. In each case however the details were almost exactly similar.

The viviparity of *H. strigosa* was observed in a single instance in the middle of July. The female was observed crawling about a fairly fresh cow-dung cake and near the edge it rapidly dropped a larva which almost immediately crawled quickly away. The new-laid larva was 3·5 mm. long and in the late 1st stage since the 2nd stage spiracles were visible under the cuticle. It was still in the 1st stage 1 hour later, but 6 hours after being laid it was found to be in the 2nd stage with the 1st stage exuvia lying beside it. The 2nd stadium is of long duration and the larva changes to the 3rd stage between 29 and 40 hours after deposition. The larva is purely coprophagous in all stages.

The habits of *H. variata* were observed four times and it seems to be a

more common species than *H. strigosa*. In each case a single larva, never an egg, was deposited in fairly fresh cow-dung. The naked larva lay inert for 2 or 3 sec., then suddenly became active and crawled away. All larvae were in the 1st stage but in one case the 2nd stage was attained within 2½ hours after being laid. A larva may reach the 3rd stage by the time it is 42 hours old, but one was still in the 2nd stage 46 hours after being laid.

The larvae of *H. variata* were coprophagous in all stages and their life cycle was also found to be much shorter than in the other dung-frequenting anthomyids described; in one instance it was completed in 21 days.

The descriptions given below of the larval stages refer to *H. variata*, but there is probably very little difference between these and corresponding stages of *H. strigosa*.

1st stage larva

The 1st stage larva is metapneustic with the posterior spiracles (Fig. 38) projecting as paired openings from the posterior face of the last abdominal segment.

In the larvae examined the 2nd stage spiracles, both anterior and posterior, were visible underlying the 1st stage cuticle, indicating the approach of ecdysis. Minute elongated spines are present over most of the surface. These are specially well developed on the posterior part of the body, on the tuberculated last abdominal segment and on the front borders of the other abdominal segments. They are very weakly developed on the anterior segments of the body except on the front border of the head where they are enlarged to form a single row of suprabuccal teeth.

The buccopharyngeal armature (Fig. 37) is rather different from the usual type. The basal piece (*B.*) is slender and deeply excavate posteriorly. Dorsally there is a large lightly chitinized area which is produced in front into the anterior dorsal bridge (*d.b.*). The ventral surface of the basal piece is also lightly chitinized. The long anterior arms are continued forward to the middle piece (*m.*) which is in such close contact with the adjacent sclerites that its form and relations are rather obscure. Running forwards from this sclerite is the large blade-shaped median dorsal sclerite (*m.d.s.*) homologous with the labrum. Ventrally are the paired *t*-pieces (*t.sc.*) homologous with the labium. Running from the points of the *t*-pieces to the under surface of the median dorsal sclerite are two straight connecting pieces (*co.p.*) which are absent from the other 1st stage larvae I have observed.

2nd stage larva

The 2nd stage larva is amphipneustic and the anterior spiracles (Fig. 40) are large and prominent and of very peculiar form. Each spiracle is partly bifid and each rounded branch bears about 15 small lobes. The posterior spiracles (Fig. 39) have two radiating slits on each side surrounded by an incomplete peritreme. The posterior face of the last abdominal segment has 12 weakly developed circumspiracular papillae.

Buccopharyngeal armature (Fig. 41). The basal piece (*B.*) is well developed and marked by the following peculiarities. The dorsal cornua (*d.c.*) are broad and bifid terminally, the upper branch being broad and lightly chitinized while the lower branch is longer, more slender and heavily chitinized. The ventral cornua (*v.c.*) are similarly bifid posteriorly, the main ventral part giving off a small hook-like upper process. The dorsal surface curves forward to merge into the reticulate anterior dorsal bridge (*d.b.*).

The middle piece is **H**-shaped in dorsal view (*M.*) and articulates closely with the basal piece behind and with the lateral hooks in front. The lateral hooks (*l.h.*) are well developed and differ from all the other 2nd stage larvae I have described in that they are not apposed but are widely separated throughout their length. Anteriorly they curve downwards and end in sharp points. Articulating with the under surface of the base on each side is a triangular piece (*d.sc.*) which occupies the same position as the dental sclerite of the 3rd stage larva.

3rd stage larva (Fig. 45)

The 3rd stage larva is amphipneustic. The anterior spiracles are similar to those of the 2nd stage and equally prominent. The posterior spiracles (Fig. 42) have three slightly divergent spiracular slits on each plate and are borne on stout projecting papillae. The general form of the larva is like that of the 2nd stage but the circumspiracular papillae are more strongly developed. Twelve of these pointed papillae are arranged in a circle round the spiracles in the same manner as in the larvae of *Calliphora* and *Lucilia*. Outside the circle are two small ventral papillae near the middle line, and more ventrally still, just posterior to the anal plate, are two large well-separated papillae. All these papillae, as well as the projecting spiracles are well seen in side view (Fig. 45).

The head (Fig. 32) is divided in front into two distinct head lobes each of which bears in front an antenna (*ant.*) dorsally and a maxillary palp (*mx.p.*) ventrally. The head lobes are continued posteriorly and ventrally as oral lobes over which the oral grooves radiate laterally and dorsally from the mouth-opening. The full-grown larva is 9 mm. long and of a yellow orange colour.

Buccopharyngeal armature (Fig. 32). The most important features of the basal piece (*B.*) are as follows. The rounded dorsal part is lightly chitinized, making the dark reticulate anterior dorsal bridge (*d.b.*) very conspicuous. Only the ventral strip of the dorsal cornua (*d.c.*) is heavily chitinized and the ventral cornua (*v.c.*) has a dorsal hook-like bifurcation. The ventral surface of the basal piece has a series of longitudinal pharyngeal ridges. From the front border a slender parastomal bar (*par.s.*) extends forwards on each side of the middle piece.

The middle piece (*M.*) which receives the terminal part of the common salivary duct (*sl.d.*) is **H**-shaped in dorsal view and massive and irregular in side view; from its front border two slender processes curve downwards and forwards.

The lateral hooks (*l.h.*), as in the 2nd stage, are separate and are capable of independent movement. Each consists of a basal portion articulating with the middle piece and having a light central area of less intense chitinization and a curved blade-like portion pointed at the tip. Not only are the hooks well separated but when they are extended or protruded the points move outwards away from each other.

Articulating with the base of each lateral hook is a roughly triangular dental sclerite (*d.sc.*) quite separate from its fellow on the other side.

The anterior spiracles, which are omitted from Fig. 32, would occupy an area extending from the middle of the anterior dorsal bridge to the ventral border of the basal piece.

The larva of *Hylemyia variata* is in all stages purely coprophagous, feeding solely on cow-dung. A comparison of its armature with that of another coprophagous anthomyid larva such as *Cryptolucilia* (Fig. 1) or *Morellia* (Fig. 36) gives, however, no indication of the very similar habits of these different larvae. In many features this representative of the lower Anthomyidae stands apart from the larvae of higher Anthomyinae (*Mydaea*, *Polietes*, etc.) and of Muscinae (*Musca*, *Stomoxys*, *Cryptolucilia*, etc.) which I have examined. On the other hand, it shows affinities with the larvae of Calliphorinae and the following points in common between it, and the larvae of *Calliphora*, *Lucilia* and *Protophormia* may show at the same time the principal characters in which it differs from the other anthomyid types described here.

The posterior spiracles are straight and slightly divergent and are surrounded by circumspiracular papillae as in Calliphorinae.

The bifurcation of the ventral cornua of the basal piece resembles that of the three calliphorines named above and the presence of parastomal bars is another feature in common. These bars are absent from the higher Anthomyidae.

The most important feature in common with the calliphorines, however, is the nature of the lateral hooks. The relation between the two hooks and the movements during feeding or locomotion are precisely similar to those of *Calliphora* and *Lucilia*. The lateral hooks of the higher Anthomyidae are always closely apposed and work together like a single piece.

The larva of *Hylemyia* shows, however, an important difference from the Calliphorinae in the presence of a well-marked detachable anal plate, a structure which is absent from the larvae of *Calliphora*, *Lucilia* and *Protophormia*.

Puparium (Fig. 111)

The puparium of *Hylemyia variata* is light brown, and barrel-shaped and is 4·5 mm. long. The anterior end is rather flattened and the larval anterior spiracles are still conspicuous at the lateral borders. The rounded posterior end with the larval posterior spiracles still bears indications of the posterior papillae.

I can find no indication either of projecting pupal spiracles or of intrapupal

or nymphal spiracles. On eclosion the puparium ruptures by the usual circular split midway round the 1st abdominal segment and by a transverse split extending round the anterior end.

Mesembrina meridiana L.

This large and conspicuous anthomyid has attracted the attention of many distinguished entomologists and it is surprising that so much of its life history and larval structure should still be unknown or incompletely described. The first detailed account of its biology is that of Portchinsky (1910) who established the viviparous habits of the female and described the larval development. Keilin (1916) made a more thorough study of the viviparity and compared it with other types among the Diptera.

Recently (1930) Keilin & Tate have described the morphology of the larva in relation to its habit and have summarized the more important contributions to our knowledge of the life history up to that date. Portchinsky's important observations have not, as far as I can ascertain, been repeated or verified in this country, and the following account of observations on the habits of *Mesembrina* and its larva, most of which were carried out quite independently and in complete ignorance of the results of other workers, may help a little towards a more complete knowledge of this familiar and widely distributed fly.

Mesembrina is probably more abundant in the dairy-farming districts of Ayrshire than anywhere else in Britain. In this area the conditions are very suitable for it in every way, since there is a great number of cattle and consequently of dung-cakes, fairly evenly distributed over the abundant pasture lands. The characteristic habit of settling on tree trunks, especially beech trees, is well known to field entomologists, and it may be seen on this place and on wooden palings and gates round fields from the beginning of May until the end of October. During the early part of the season it shares this habitat with the green Tachinid *Gymnochaeta viridis* and with *Leptis* sp., while at the end of the season it occurs mainly along with *Polietes lardaria*. Other sources of attraction are hedge trimmings, rhubarb leaves, the flowers of golden rod (*Solidago*) and faded roses.

Apart from these various habitats, *Mesembrina* is found principally on cow-dung in the fields from the middle of May till the beginning of October. On these dung-cakes it may be seen copulating and ovipositing. Without going into unnecessary details the process of oviposition is briefly as follows: the extremely large smooth white egg, 4·5 mm. long, is laid in the dung so that its more pointed anterior end is left exposed, and, coincident with laying, the egg splits open and the newly hatched larva immediately burrows down into the dung leaving the soft crumpled chorion lying on the surface. In the large number of cases where this act of oviposition has been watched in the field, the details have always been almost identical, never more than one egg is laid at a time and the total number of eggs laid by one female is only about

four or five. This process described above has been called ovo-larviparity or ovo-viviparity although it is probably more viviparous than oviparous since the egg stage has no real external existence, the chorion being as it were a useless ancestral relic which is disposed of at the first convenient moment.

The egg (Fig. 143) is of the normal smooth *Musca* pattern and differs only in size from that of *Cryptolucilia*, *Morellia*, etc. On the dorsal surface are two faint parallel longitudinal ribs bounding a narrow dorsal strip. When the egg hatches the chorion is ruptured along a line just outside one of these ribs. The ventral surface is convex and the dorsal surface is more flattened. The anterior end is slightly more pointed and tapering than the posterior end. The newly hatched larva is in the great majority of cases in the 1st stage, but I have observed a single case in which a 2nd stage larva hatched from the egg, eclosion and ecdysis being in this case coincident.

1st stage larva

The 1st stage larva is metapneustic. The posterior spiracles (Fig. 59), which protrude from the posterior face of the last abdominal segment, are small paired openings each of which may be divided terminally either partly or completely into two by a septum.

On the anterior borders of abdominal segments II–VII are broad ventral bands of spines continued about two-thirds of the way up the side.

Buccopharyngeal armature (Figs. 56, 57). This consists of the following sclerites. The delicate pharyngeal sclerite or basal piece (*B.*) has slender pointed dorsal cornua and broader ventral cornua. The large anterior dorsal bridge (*d.b.*) forms a complete arch connecting the two lateral plates. The basal piece extends forwards as two slender parallel arms which articulate distally with the 1st stage middle piece (*m.*) of the usual shape.

The median dorsal sclerite (*m.d.s.*) is a large blade-like piece lying above the buccal cavity; in this preparation (Fig. 56) it is seen to have a distinct bifid origin, articulating with each arm of the middle piece by a slender posterior process. This sclerite, which is regarded as homologous with the labrum, is found in all other 1st stage anthomyid larvae but the basal articulation is seldom so clear as in *Mesembrina*. Forming the sides and floor of the buccal cavity there are two pairs of sclerites. As well as the paired *t*-pieces (*t.sc.*), which are usually present alone in 1st stage anthomyid larvae and are considered to be homologous with the labium or lower lip (Keilin, 1915), there is here, lying ventral to these, an additional pair of *t*-shaped sclerites (*to.sc.*), which form the lateral borders of a flat tongue-like sclerite with a spiny anterior border. This skeleton is described mainly from the exuvium of the 1st stage larva, thus ensuring that there are no rudimentary or incipient 2nd stage sclerites present. Of the other 1st stage anthomyid larvae which I have examined, this additional lower lip occurs only in that of *Polietes hirticrura*, and in a less well-developed state. Its exact homology is doubtful.

The duration of the 1st stadium is subject to great variation but generally

it is shorter than that of other anthomyids. Occasionally, as has been mentioned, the larva on hatching from the egg is already in the 2nd stage, but on the other hand I have watched ecdysis taking place 12½ hours after hatching and between these two extremes every possible gradation has occurred. The average length, however, is 3–5 hours.

A conspicuous feature of the late 1st stage larva, and one which is absent from the 2nd stage, is the black dorsal bridge of the basal piece which can be seen through the transparent skin of the larva.

2nd stage larva

At the commencement of this instar the larva is about 7 mm. long and is amphipneustic. The anterior spiracles have the full number of lobes, 16–18, while the pale coloured posterior spiracles (Fig. 71) have two folded spiracular slits in each plate. The general form of the larva is very like that of the 1st stage.

The buccopharyngeal armature (Fig. 70) differs considerably from that of the 1st stage. The basal piece (*B.*) is larger and more solidly built and the dorsal arch (*d.b.*) is not complete, the upward projections from each lateral plate only being connected by a very slight transverse band. The anterior arms of the basal piece are connected ventrally by a strong transverse arch. The middle piece (*M.*) is now of more usual form and receives ventrally the terminal part of the common salivary duct. There are no paired pieces immediately in front of the middle piece corresponding to the angular sclerites of *Cryptolucilia* and others.

The paired lateral hooks (*l.h.*) are long and slender and closely apposed distally, but are separated proximally where they articulate with the middle piece. Ventrally there are two pairs of sclerites which occur in many other 2nd stage anthomyid larvae. A pair of irregular closely approximated pieces (*a.sc.*) lie just under the tip of the lateral hooks, while just behind these is a pair of stout and distinctly separate pieces (*l.sc.*) corresponding to the labiate sclerites of *Cryptolucilia*. The 2nd stage larva normally undergoes ecdysis about 35 hours after hatching, though naturally this time is liable to vary.

3rd stage larva

Keilin & Tate (1930) have recently described this stage of the larva so I will confine the present account to a brief survey emphasizing those characters which are of adaptive or systematic importance. The larva is amphipneustic and the anterior spiracles have 16–18 lobes (Fig. 60) and a conspicuous black external scar (*ex.s.*). This number is exceptionally large and forms a feature which would in itself be sufficient to separate this from all other anthomyid larvae described.

The posterior spiracles (Fig. 21) are large and well separated. The spiracular slits are folded to an even greater extent than in *Cryptolucilia* and *Dasyphora*, and while the general pattern of the sinuous slits is constant and specific, there

are minor individual variations, an example of which can be appreciated by comparing my example (Fig. 21) with that of Keilin & Tate (1930, p. 177, Text-fig. IV (3)). These spiracles in the mature larva are more heavily chitinized than in the early 3rd stage, the external scar and peritreme being no longer distinct. The anal plate (Fig. 72) is well developed and of the normal curved shape. When mature, the yellowish larva of *Mesembrina* is the largest dung-frequenting maggot, measuring 20 mm. in length.

Buccopharyngeal armature (Figs. 66–69). The basal piece (*B.*) when compared with that of *Cryptolucilia* is seen to be more elongated, with a deep recess between the dorsal and ventral cornua. The latter (*v.c.*) show peculiar and fairly constant dark lines of heavier chitinization. At the anterior end the dorsal bridge (*d.b.*) curves over the prominent projection which articulates with the middle piece (*M.*). The middle piece is rather shorter and more solid than that of *Cryptolucilia* and has in addition a pair of peg-like processes at the anterior end. The paired lateral hooks (*l.h.*) are sharply pointed and curved with large basal parts.

Ventrally are the paired oral bars (*o.b.*) lying external to and mostly behind the paired anterior rods (*a.r.*) which are toothed on their inner faces. The action and function of these parts can best be appreciated from a comparison of the two figures (Figs. 67, 68) which show the lateral hooks in their normal retracted position and in their extended state. The anterior rods with their toothed margins obtain a firm grip which enables the pointed hooks to work to and fro and enlarge the opening in the body wall of the prey. The median ventral arch (*m.v.a.*) is a complete arch thereby differing from the coprophagous larvae of *Musca*, *Stomoxys*, *Cryptolucilia*, etc., where it takes the form of two separate dental sclerites. It resembles on the other hand the very similar completely arched sclerite of *Muscina*, *Myiospila*, *Mydaea*, and all other carnivorous and semi-carnivorous larvae.

Keilin (1917) has shown the close relation between the construction of the buccopharyngeal armature and the habits of the larvae of anthomyids in general and his conclusions can be applied very effectively to the larvae of *Mesembrina*.

Both Portchinsky (1910) and Séguy (1923) regarded *Mesembrina meridiana* as being purely coprophagous. Keilin & Tate (1930), from a study of the skeleton and in the absence of any other definite observations, included it among the semi-carnivorous larvae. In the buccopharyngeal armature are found features which are peculiar to both carnivorous and saprophagous types. The structure of the lateral hooks, the presence of well-developed accessory buccal sclerites, and above all the complete form of the median ventral arch are all features of a true carnivore. On the other hand, the general form of the hypostomal and pharyngeal sclerites, together with the presence of a series of longitudinal pharyngeal ridges on the lightly chitinized ventral surface of the basal piece, indicates a coprophagous or at the most a semi-carnivorous habit. On the characters of the skeleton alone therefore

we would be quite justified in concluding that this larva is a facultative carnivore.

The results of observations and breeding experiments are not exactly conclusive since the larvae can only be conveniently bred and observed in highly artificial conditions. The larva of *Mesembrina* can be reared from the egg to the adult in a completely isolated culture of pure cow-dung, and in this pabulum it lives and thrives like any other purely coprophagous larva, becoming fully grown in 15–17 days. On one occasion, however, an immature *Dasyphora* larva was introduced to an active early 3rd stage *Mesembrina* larva which had been derpived of dung for 2 days. The *Dasyphora* larva was immediately attacked and consumed and from that time onwards the *Mesembrina* larva behaved as a true carnivore, refusing to feed on anything but living maggots. Other dung-frequenting larvae were treated in a similar way; larvae of *Cryptolucilia* and *Haematobia* were equally acceptable, but those of *Morellia* were left untouched as they also are by *Myiospila* and *Mydaea*. In 11 hours ten *Cryptolucilia* larvae, each about 8 mm. long, were entirely consumed by one larva, and during the entire 3rd stage a single *Mesembrina* larva devoured 46 3rd stage *Cryptolucilia* larvae as well as six other small anthomyid larvae. The exact mode of life in the field under natural conditions is almost impossible to determine, and whether it lives a coprophagous or a carnivorous mode of life or a combination of these two must depend on a number of factors which it is impracticable to reproduce artificially. The experiments described above suggest, however, that its true mode of life is that of a facultative carnivore preying on other dung-larvae in the community whenever the opportunity occurs.

When fully grown the sluggish larva is yellowish in colour due to the deposition of fat throughout the body cavity, and it is found at the bottom of the dung-cake next to the earth. Normally by this time the dung-cake has dried considerably, and pupation takes place in the almost solid material at ground level. In artificial cultures pupation usually takes place in the earth Larvae found in dung from the middle of September onwards do not pupate at once, they tide over the winter in the larval stage and may be found hibernating in dung-cakes during the winter months. The puparium is often enclosed in a smoothly lined cell of dried dung. This is merely a space hollowed out by the larva and bears no relation or resemblance to the earth cocoon of *Muscina*.

Puparium (Fig. 46)

The puparium is of unusual size and shape. It is the largest of all the anthomyid puparia examined, being as much as 14 mm. long, and exceeding in length even the puparia of the Calliphorines, *Calliphora*, *Lucilia*, and *Protophormia*. It is not round in section but has the lateral surfaces prominent, forming two lateral ridges. In shape it bears the same relation to the puparia of *Musca*, *Stomoxys* and most other Muscinae as the similarly ridged puparium of *Protophormia terranovae* does to those of *Lucilia* and *Calliphora*.

The prothoracic nymphal spiracles (Fig. 47) project as exceedingly small pupal horns which are almost impossible to distinguish externally since they are situated not, as is usual, on the sides of the 1st abdominal segment, but in the furrow between the 1st and 2nd abdominal segments. The flattened circular posterior face of the last abdominal segment with the larval posterior spiracles is surrounded by a narrow rim. The anal plate of the larva has become very heavily chitinized and separates easily from the rest of the puparium. On eclosion the puparium opens in the normal way. The pupal period lasts about 16 days in summer.

Polietes hirticrura Meade

The biology of the two common species of *Polietes*, *P. lardaria* F. and *P. albolineata* Fallen, has been worked out by Portchinsky (1910) and Séguy (1923), while the morphology of their larvae has been described by Keilin (1917) and in more detail by Keilin & Tate (1930). Besides these two species there is another British one, *P. hirticrura* Meade, whose biology and habits apparently have not up till now been observed. This anthomyid was first described by Meade (1887), and later (1897) he says that "only the male is known of this rare species". *P. hirticrura*, however, is by no means rare in Ayrshire and I have captured and observed a number of females as well as males.

In the *West of Scotland Fauna List* (1901) this fly is also recorded by Verrall from Kilmarnock, which is the area in which I myself have studied it. Furthermore in the King Collection in the Zoology Department of Glasgow University there are three females and one male from Aviemore.

While this species bears a general resemblance to *P. lardaria* and *P. albolineata* it has a quite distinctive appearance, due to the bright steel-blue body colour, together with the orange colour of the calyptera and wing bases, which can be even more appreciated in the field.

The majority of the males are seen settled on the trunks of beeches and other trees from the beginning of May until September; this seems to be one of their most characteristic habits and only a few have been seen on hedges or wooden fences round fields. The females are seen either with the males or on cow-dung.

The ovipositing habits of *P. hirticrura* are interesting as they differ from those of nearly all other coprophagous anthomyids.

The gravid females alight for preference on fairly fresh cow-dung and I have seen as many as four on one dung-cake. They always crawl over the surface with the long ovipositor protruded and trailing, and this habit is a sure indication that oviposition is about to take place. The eggs, however, are never laid on or in the dung like those of *Cryptolucilia* and *Morellia*, but the females crawl over the edge of the cake down into the grass and there, quite out of sight, deep among the grass roots, they lay their eggs on the damp shaded ground beside the dung-cake. This seems to be an unvarying habit and is

shared by the closely related *Polietes lardaria* alone among the many coprophagous flies I have observed.

In this respect it is interesting to note that the common Syrphid *Rhingia campestris*, whose habits I have studied, lays dense masses of eggs on the underside of clover leaves and blades of grass overhanging the edge of cow-dung cakes. The larvae on hatching immediately drop, often a distance of several inches, on to the hard surface skin of the dung and, after finding a crack or fissure to burrow into, they spend the larval stages as coprophagous types.

The eggs of *Polietes hirticrura* are laid in loose batches which may consist of as few as four eggs or as many as seventeen. The number seems to be very variable and I have watched an ovipositing female leave the cake and fly away only to return shortly afterwards to resume ovipositing at once in exactly the same place where it left off.

The egg (Fig. 148) is pure white, very like that of *Cryptolucilia* or *Musca*, with faint parallel ribs on the dorsal surface and with no conspicuous surface markings. It is 2 mm. long, slightly smaller than that of *Polietes lardaria*. On hatching the dorsal strip becomes free like a tongue, attached only at the posterior end.

Two separate batches of eggs, laid at the end of July and the third week of August, took 44 and 30 hours respectively to hatch. All newly hatched larvae were in the 1st stage.

1st stage larva

The 1st stage larva in external appearance is very like that of the other anthomyids described. It is truncate posteriorly and tapers towards the anterior end, and consists of a head segment, three thoracic segments and eight abdominal segments. The larva is metapneustic. The posterior spiracles (Fig. 63) project from the posterior face of the last abdominal segment, and each spiracle has a single opening surrounded by palmate branching hairs (*pal.h.*). There are no spines on the thoracic and 1st abdominal segments, but distinct ventral spine pads are present on the anterior borders of abdominal segments II–VII.

The head (Fig. 61) is provided with paired antennae (*ant.*) and maxillary palps (*mx.p.*).

Buccopharyngeal armature (Figs. 61, 62). The basal piece (*B.*) is of typical 1st stage form, it is deeply excavate posteriorly and extends backwards as the slender, pointed, diverging dorsal and ventral cornua. The two lateral plates are connected by a weakly chitinized but complete anterior dorsal bridge (*d.b.*). The basal piece extends forwards as a pair of slender arms which embrace distally the middle piece.

The middle piece (*m.*) in dorsal aspect is H-shaped, with the connecting transverse bar situated near the posterior end. Anterior to the middle piece is the median dorsal sclerite (*m.d.s.*) homologous with the labrum, and extending from the base of this piece to the mouth-opening are two pairs of sclerites which seem to correspond with the similarly placed sclerites of the 1st stage

Mesembrina larva. In addition to the usual paired *t*-pieces (*t.sc.*) there is a pair of lateral pieces (*to.sc.*) which, however, are not apparently connected to form a flat tongue-like sclerite as is the case in *Mesembrina*.

The 1st stage larva is purely coprophagous. Larvae, bred during August, examined 21 hours after hatching, were still in the 1st stage, but examined 24 hours after hatching some were found in the 2nd larval stage and one was observed actually moulting. Larvae of another culture were all found to have attained the 2nd stage within 24 hours of hatching and were at this time about 3·5 mm. long.

2nd stage larva

The 2nd stage larva is amphipneustic with 5-lobed anterior spiracles. The posterior spiracles (Figs. 64, 65) are of very unusual and quite characteristic appearance. The spiracular plates, which are heavily chitinized compared with other 2nd stage larvae, are large and roughly oval in shape, with a concavity on their inner adjacent borders. In each plate the two spiracular slits are slightly curved and almost parallel; round the periphery are seven large clear openings probably of perispiracular glands (*ps.gl.*). Six of these are round or slightly oval in shape and equal in size, while the seventh is distinctly larger and is drawn out into a point directed towards the centre of the plate. Radiating hairs in connexion with these are present round the edge of the plate.

No other 2nd stage larva which I have examined has posterior spiracles of this nature. While this is a valuable diagnostic feature, on the other hand, as is so often the case with the spiracular characters of anthomyid larvae, it seems to bear no relation to the systematic position of the adult.

Buccopharyngeal armature (Fig. 79). The basal piece (*B.*) is well developed and heavily chitinized except for a light triangular area on the front border of the dorsal surface.

There is a deep indentation posteriorly, and the straight dorsal cornua (*d.c.*) run almost parallel to the ventral cornua (*v.c.*). The anterior dorsal bridge (*d.b.*) has the form of a complete, distinctly reticulate or perforate, arch arising from each side by a slender stalk.

The forward projecting arms of the basal piece are connected by a transverse ventral bar (*t.v.a.*). The middle piece (*M.*) is well developed, H-shaped in dorsal view and triangular in side view. Arising immediately in front of, and extending back over, the middle piece, is a pair of angular sclerites (*an.s.*) corresponding to those of the 2nd stage *Cryptolucilia* and *Dasyphora* larvae.

The lateral hooks (*l.h.*) are closely apposed and very slightly curved anteriorly; posteriorly they are distinctly separate at the bases which are in close contact with the angular sclerites. Ventrally there are two pairs of sclerites, the large separate labiate sclerites (*l.sc.*) posteriorly and a pair of closely approximated accessory sclerites (*a.sc.*) of doubtful homology, anteriorly.

The 2nd stage larva, like the 1st stage one, is purely coprophagous, living entirely on the cow-dung. Larvae of three separate cultures examined 52, 53

and 54½ hours respectively after hatching were all still in the 2nd stage but obviously near the end of the stadium, since 3rd stage lateral hooks could be distinctly seen overlying the 2nd stage skeleton. This stadium therefore lasts about 30 hours. Without referring to skeletal features or spiracular slits the early 3rd stage larva can easily be distinguished from the similar sized late 2nd stage larva by having yellow posterior spiracles compared with the prominent intensely black spiracles of the latter.

3rd stage larva (Fig. 73)

The 3rd stage larva is amphipneustic. The anterior spiracles (Fig. 75) have 5 lobes on each side and a conspicuous external scar (*ex.s.*) like that of *Mesembrina*. The larva of *Polietes lardaria*, on the other hand, usually has 10-lobed anterior spiracles. The posterior spiracles (Figs. 74, 76) are large and rounded with the internal adjacent borders of the spiracular plates flattened.

In the mature larva the plates are not heavily chitinized as in *Mesembrina*. The peritreme is distinct as also is the round external scar situated near the inner border of the plate.

In each plate there are three sinuous spiracular slits which show about the same degree of folding as those of *Stomoxys*, and four round clear openings of perispiracular glands. The external appearance of the full-grown larva is very like that of *Polietes lardaria* as well as *Myiospila* and *Mydaea*, not only because of the similar pale creamy colour but also on account of the smooth body surface and gently rounded last abdominal segment. Without examination of the spiracles it is very easy to confuse the larvae of these different species when they are alive. The mature larva of *Polietes hirticrura* is 15 mm. long. Double ventral bands of spines are present on the anterior borders of abdominal segments II–VII. On the ventral surface of the last abdominal segment is a well-developed anal plate of the usual type resembling closely that of *P. lardaria*.

Buccopharyngeal armature (Fig. 80). In the general form and relation of its component parts this skeleton bears a close resemblance to that of *Mesembrina* while it differs strikingly from that of the closely related *Polietes lardaria*.

The basal piece (*B.*) is very like that of *Mesembrina* but differs in a few details. The dorsal cornua (*d.c.*) are slightly longer than the ventral cornua (*v.c.*) while in *Mesembrina* they are distinctly shorter.

In *Mesembrina* the ventral cornua rises into a point dorsally, whereas in *Polieta hirticrura* this part is greatly enlarged and rounded. The bands of heavy chitinization follow a different scheme in the two species. The ventral surface of the basal piece is similarly marked with a series of longitudinal pharyngeal ridges.

The middle piece (*M.*), which receives ventrally the terminal part of the common salivary duct, is short and massive, articulating with the basal piece.

As in *Mesembrina* the middle piece bears anteriorly a forward projecting ventral process on each side.

The lateral hooks (*l.h.*) are also very similar to those of *Mesembrina*. Ventral to these is a pair of oral bars (*o.b.*) lying behind and external to a pair of anterior rods (*a.r.*) which curve round in front of the tips of the lateral hooks.

The median ventral arch (*m.v.a.*), as in *Mesembrina* and all other semi-carnivorous and carnivorous anthomyid larvae, forms a true compact arch.

Since there is such a close resemblance between the buccopharyngeal armature of *Polietes hirticrura* and that of *Mesembrina* in the 3rd stage, we would be justified—as Keilin has shown—in concluding from structure alone that the habits of these two larvae were very similar.

Observations and experiments on the larvae have shown that this conclusion is on the whole correct.

The 3rd stage larva of *Polietes hirticrura* is a facultative carnivore, which may grow to the adult state feeding coprophagously on dung alone or which may, and usually does, live a semi-carnivorous existence preying on other larvae in the dung-cake whenever the opportunity arises. *Cryptolucilia* larvae introduced into a culture of *Polietes hirticrura* are not usually attacked at once as in the case of *Myiospila*, but if they are left undisturbed they are eventually entirely consumed. Three *Cryptolucilia* larvae introduced to six much smaller larvae of *Polietes hirticrura* were completely demolished overnight. In one instance a *Cryptolucilia* larva introduced to a single *Polietes* larva was attacked at once in the bright light after the fashion of *Myiospila*. A certain amount of cannibalism occurs in overcrowded cultures and the number of larvae which reach the 3rd stage is usually found to be much less than the number of eggs that hatched—ten out of twenty-five in one instance. I have bred larvae to maturity on a diet of pure dung alone, and larvae which were given living food in the early 3rd stage can be brought to maturity on pure dung during the latter half of the 3rd stage.

In this respect *Polietes hirticrura* differs strikingly from *P. albolineata* whose larval habits I have not observed but which, according to Portchinsky (1910) and Séguy (1923), is the most carnivorous of all carnivorous forms.

The winter is passed in the larval state as is the case with *P. lardaria*. Larvae of *P. hirticrura* found in cow-dung on 3 January emerged as adults on 5 May, exactly the same day that *P. lardaria* emerged from larvae found in cow-dung on 27 October. I have not noted the exact length of the pupal period, but full-grown larvae taken from dung in the fields emerged as adults 18 days after, giving a rough indication of the duration of this stage.

Puparium (Fig. 77)

The puparium is roughly barrel shaped but it tapers more towards the posterior end than that of *Cryptolucilia* or *Musca*. The larval head and first two thoracic segments are compressed to form a prominent knob at the front

end. The posterior face of the last segment is round and flattened, rather like that of *Mesembrina*, and bears the larval posterior spiracles. The anal plate is distinct and detachable. The prothoracic nymphal spiracles (Fig. 78) project to the exterior as pupal horns dorso-laterally just in front of the border between abdominal segments I and II. The puparium is 8 mm. long and eclosion occurs in the usual manner.

The puparium of *Polietes lardaria* is about 9 mm. long. It has the last segment smoothly rounded, not flattened, posteriorly, and the anterior segments are not consolidated to form a knob. In other details it is similar to that of *P. hirticrura* described above.

Myiospila meditabunda F.

The biology of this fly was first worked out in Russia by Portchinsky (1910) who established the carnivorism of the larva and the existence of only two larval stages instead of the normal three.

A summary of his results is given by Keilin (1917) who has also verified the carnivorous habits and has described in more detail the morphology of the 3rd stage larva and the formation of the cocoon. Apart from Portchinsky's no other observations have been made on the natural ovipositing habits of this fly or on the early stages of the larva.

Myiospila, like *Mesembrina meridiana*, is probably as abundant in the dairy-farming districts of Ayrshire as anywhere else, and only this fact has made it possible for me to investigate the life history in detail.

The dull coloured females have few characters which make them easy to recognize in the field; they are in general appearance so like many other inconspicuous grey anthomyids that it is often necessary to approach close enough to examine the characteristic curvature of the fourth longitudinal vein before they can be identified with certainty. The males on the other hand, though less common, are easily recognized, apart from the wing venation, by the very dark faintly striped thorax, the dark wings, and the four large black spots on the abdomen.

Myiospila may appear as early as the second week of April, but it is not till the end of May that it becomes frequent. In the early part of the season males and females occur together on bushes and hedges, but from the end of May onwards the females are almost entirely restricted to cow-dung on which the males are also found as well as on fences round the fields. In summer nearly every dung-cake, except those that have dried hard and white, has a few females on it, but however long or frequently they are observed they are never seen to oviposit. It is only by watching freshly dropped dung that the females can be seen laying eggs. About a quarter of a minute after the dung is dropped *Haematobia* appears, lays its eggs and a few minutes later flies away again. While there are still one or two of these flies left on the dung, females of *Myiospila* begin to appear, and each of them lays a single egg and

then flies away. More females continue to arrive and about 2 min. after deposition of the dung there may be as many as half a dozen females ovipositing at the same time. Then gradually the numbers fall off and by the time the dung is 15–20 min. old there are none left on it. After the dung has dried for a short time, they appear again but not to oviposit. I have observed these habits on numerous occasions and have found them to be remarkably constant. Only once have I seen a female ovipositing on old dung, and only very occasionally does a female lay more than one egg on the same dung-cake. *Haematobia* and *Myiospila* are evidently equally attracted by freshly dropped dung and the few minutes difference between the times of arrival of the two flies is almost certainly due to *Haematobia* on the cow becoming aware of the dung sooner than *Myiospila* settled on the older scattered cakes in the field. The egg is laid in such a way that the dorsal part of the anterior end projects a little above the surface and can be seen fairly easily with the naked eye. Females may be induced to oviposit in captivity but only if they are captured just before ovipositing in the field, and only if the same fresh dung is used.

The egg (Fig. 152) is about 2 mm. long and of quite distinctive appearance. It has well-developed dorso-lateral flanges which gradually widen towards the anterior end where they project forwards on each side. The ventral surface is convex and smooth with faint honeycomb markings on the chorion. The flanges together with the space between them form a dark, flat, tapering dorsal strip or lid which on hatching of the egg lifts up like a trap-door till the larva has crawled out, then falls back into place again.

In one case eggs took as long as 52 hours to hatch, while in another, and probably more typical case, they took exactly 24 hours to do so at an average temperature of 25° C.

Portchinsky described the newly hatched larva as being in the 1st stage, and considered that the 2nd stage was omitted from the life history.

For various reasons stated below I am convinced that Portchinsky's 1st stage *Myiospila* larva is really a 2nd stage larva and as such I have described it.

2nd stage larva

The newly hatched larvae were in every case in the 2nd stage. The 2nd stage larva is amphipneustic with 4-lobed anterior spiracles (Fig. 83). The posterior spiracles (Fig. 81) are small, very black, paired openings on the posterior face of the last abdominal segment, and are of true 1st stage type. In most cases the incipient 3rd stage posterior spiracles can be seen underlying the cuticle and frequently the three radiating spiracular slits can be distinguished.

A double band of spines is present on the anterior borders of the ventral surface of abdominal segments I–VII. Spines are also present on the ventral surface of the last segment.

The head bears paired antennae and maxillary palps.

Buccopharyngeal armature (Fig. 85). The basal piece (*B.*) is well developed and has strong dorsal and ventral cornua, the latter not being slender and

pointed as is usually the case with 1st stage larvae. The anterior dorsal bridge (*d.b.*) is incomplete and its two lateral arms, projecting dorsally, are quite separate. The basal piece is not drawn out into long anterior arms as in normal 1st stage larvae, but has an ordinary sloping articulation with the intermediate piece. The intermediate piece (*M.*) is quite distinct with two well-developed lateral plates as in 2nd stage anthomyid larvae. The lateral hooks (*l.h.*) are long, nearly straight, and closely apposed distally, though obviously paired near their bases. Lying ventral to these are two elongated pieces (*l.sc.*) more than half the length of the hooks. This armature shows in all its component parts more resemblance to that of a typical 2nd stage anthomyid larva than to a 1st stage one.

The absence of the long anterior arms of the basal piece, the distinctness of the intermediate piece and the absence of that characteristic 1st stage sclerite, the median dorsal sclerite, are all 2nd stage features. The paired pieces (*l.sc.*) ventral to the lateral hooks would therefore correspond to what I have called the labiate sclerites of other 2nd stage larvae.

Portchinsky, who does not figure this skeleton, described the larva as being in the 1st stage; but, despite the nature of the posterior spiracles, I consider that the structure of the buccopharyngeal armature and the presence of anterior spiracles are sufficient evidence to classify it as a 2nd stage larva, in which case the 1st stage has been suppressed from the life history.

The presence of only two larval stages is best verified by watching the larva just before and during ecdysis. The posterior spiracles, the 3rd stage anterior spiracles, and the 3rd stage armature are all visible under the cuticle of the late 2nd stage larva, and the larva after moulting is in the 3rd stage with the same armature and spiracles as the full-grown larva. The length of the 2nd larval stage seems to be very variable; on the one hand moulting was found to take place as soon as 9 hours after hatching and, on the other hand, a larva did not change to the 3rd stage till between 26 and 30 hours after hatching. The 2nd stage larva is coprophagous and the brown contents of its gut can be seen through the semi-transparent cuticle.

3rd stage larva

This larval stage has already been described by Keilin (1917) and I will only mention those characters which I consider to be of importance in the present discussion.

In the fully grown larva the relatively small size of the posterior spiracles (Figs. 106, 108) is a certain indication—as in *Mydaea*, *Hebecnema*, and *Phaonia variegata*—that the 3rd stage is reached at a comparatively early stage in development. Larvae which pass through three stages have always relatively large posterior spiracles, e.g. *Mesembrina*, *Cryptolucilia*, and *Dasyphora*. In the buccopharyngeal armature the late 3rd stage larva has more extensive dorsal cornua than in the early 3rd stage. The median ventral sclerite forms a true arch as in all carnivorous and semi-carnivorous larvae.

I have found the 3rd stage larvae of *Myiospila* to be very carnivorous, attacking and destroying larvae of *Cryptolucilia*, *Haematobia*, and *Dasyphora*, but not those of *Morellia*. They also attack each other readily in the absence of other food, and in cultures each larva has to be bred separately to prevent cannibalism.

Unlike Portchinsky I have been unable to breed larvae for any length of time, much less to maturity, on dung alone, and I have always found them to be obligative carnivores entirely dependent on living prey.

The puparium and the formation of the cocoon have been described by Keilin (1917). I have repeated these observations and have noticed in addition that fully grown larvae, removed from the dung or earth and put between clean double watch-glasses, form a pure silken cocoon which has naturally no foreign particles adhering to it, and which, on account of the sticky secretion, is firmly fixed to the glass. This should be compared with the contrasting habits of the larvae of *Muscina pabulorum*.

In four separate cases I found the pupal period in July and August to last 17, 18 and 19 days respectively.

It is unfortunate that the voracious carnivorism of *Myiospila* larvae should be of so little economic value, since, apart from *Haematobia*, the larvae it normally feeds on are those of quite harmless dung-frequenting flies. Over a long period I have never seen *Myiospila* anywhere near the farm middens where *Musca* and *Stomoxys* breed extensively. The latter flies in their turn never oviposit or breed in the fields where *Myiospila* is. The principle food of the *Myiospila* larva is undoubtedly the larvae of *Cryptolucilia* which are abundant in every dung-cake. A certain proportion of *Haematobia* larvae must also be destroyed but, since their numbers in each cake are insignificant compared with those of *Cryptolucilia*, this cannot be regarded as a very important controlling factor.

Mydaea urbana Mgn.

Our only information about the biology of this species is due to Portchinsky (1910) who followed out the essential parts of the life history and established the carnivorous habits of the larvae. A brief summary of his results has been given by Keilin (1917) and, excluding the figures, that is the only part of his work with which I have been able to compare my own observations. *Mydaea urbana* is one of the least common dung-frequenting flies in Ayrshire, although it is much more frequently seen on the island of Arran where the dairy farms and cattle are practically restricted to a relatively narrow coastal area of pasture land. Females, and occasionally males, occur on cow-dung cakes in the fields during the warmer summer months, and the life history can be followed by observing the habits of the gravid females. The ovipositing habits of *M. urbana* are very different from those of *Myiospila*, although the subsequent life histories of these two species are remarkably similar. The females show no marked preference for freshly dropped dung but are usually found

on dung dropped either that day or the night before. The eggs are laid singly, and as many as 26 have been found distributed over the surface of one cake.

In the few cases I have observed the females appear to lay all or most of their eggs in a single cake and do not distribute them over such a wide area as *Myiospila* does. The egg is inserted in the dung in such a way that the anterior end is left projecting slightly above the surface, and can be seen from above without disturbing the dung.

The egg (Fig. 150) is of quite distinctive form; it has well-developed lateral flanges which are produced anteriorly into long pointed processes with serrated outer margins. In addition there is a median pointed process at the anterior end, which extends forwards as far as the lateral processes and is serrated along both margins. The total length of the egg is 3 mm., and the distance between the tips of the lateral horns is 1 mm. The dorsal surface between the flanges is flattened, the ventral surface is convex. On hatching, the whole dorsal strip lifts up like a trap-door, as in *Myiospila*, and falls back into place again when the young larva has crawled out. The three anterior processes together with the large size enable this egg to be distinguished at a glance from those of all other dung-frequenting flies. In August and September two separate batches of eggs took 54 and 52 hours respectively to hatch.

The newly hatched larva is amphipneustic and according to Portchinsky is a 1st stage larva. However, I consider, as I have done in the case of *Myiospila*, that this larva is in the 2nd stage, and as such I have described it below, paying special attention to those features which in other anthomyid larvae are peculiar to the 1st or to the 2nd stage.

2nd stage larva

The larva on hatching from the egg is already amphipneustic. The anterior prothoracic spiracles (Fig. 84) are 4–5-lobed, and the posterior spiracles (Fig. 82, *p.sp.*), as in *Myiospila*, project as black paired openings from the posterior face of the last abdominal segment. The posterior spiracles are like those of a typical 1st stage anthomyid larva, and below the cuticle can frequently be seen the large 3rd stage spiracles with three slightly divergent spiracular slits. On the anterior borders of abdominal segments I–VII are well-developed bands of short pointed spines (Fig. 86), and there is also a band of spines on the hind border of segment VII. The head bears paired antennae and maxillary palps.

Buccopharyngeal armature (Fig. 87). This is made up of the same components as the corresponding stage of *Myiospila*. The basal piece (*B.*) has the same proportions and appearance but with this important difference, that the anterior dorsal bridge, incomplete in *Myiospila*, is here completely absent. In all other 1st and 2nd stage anthomyid larvae examined the anterior dorsal bridge is present in some form or other. The whole basal piece is lightly chitinized. The middle piece (*M.*) is boat-shaped, being made up of two lateral plates sloping inwards ventrally and connected by a transverse piece. The

central part of each plate has disappeared, leaving an elongated opening. The lateral hooks (*l.h.*) are not so well developed as in *Myiospila* and take the form of separate slender bars running forward to meet at their tips. Lying ventral to the hooks and extending forwards from their bases is a pair of stout sclerites (*l.sc.*) which, as in the case of *Myiospila*, I consider to be equivalent to the labiate sclerites of other 2nd stage larvae. They are better developed in this case and are clubbed distally. Extending between these clubbed ends and the tips of the lateral hooks is an accessory piece (*a.sc.*), but I have not been able to determine its exact relations with the other sclerites, and whether it is paired or unpaired. It is furnished at the tip with slightly recurved teeth. This armature in all its parts is just a further modification of the *Myiospila* type, and the same features of that larva which were used to demonstrate the 2nd stage nature of the armature are equally apparent in this case. Here again we note the absence of long anterior prolongations of the basal piece, the presence of a well developed and separate middle piece, the absence of a median dorsal sclerite and the presence of distinct though weakly developed lateral hooks. Although the posterior spiracles are of 1st stage type, the presence of anterior spiracles, together with the skeletal characters described above, point to the conclusion that the newly hatched larva of *Mydaea urbana* is in the 2nd stage and that it is the 1st stage which has been suppressed from the life history. The presence of only two larval stages separated by a single ecdysis was established in precisely the same way as in *Myiospila*. The duration of the 2nd stadium seems to be fairly short in *Mydaea*; traces of 3rd stage armature and spiracles are often visible through the cuticle of the newly hatched larva. One larva examined 3 hours after hatching was already in the 3rd stage, with the 2nd stage exuvium still adhering to it. On the other hand, a larva examined 7 hours after hatching was still in the 2nd stage with no indications of underlying 3rd stage structures.

3rd stage larva

The 3rd stage larva is amphipneustic. The anterior spiracles have 4–5 lobes and the posterior spiracles (Fig. 107) have on each side three radiating, elongate oval, spiracular slits. In the early 3rd stage the posterior spiracles are very like those of *Myiospila* (Fig. 108) with the narrow peritreme, the circular external scar and the four openings of perispiracular glands. In the mature 3rd stage larva the spiracular plates have become heavily chitinized so that the peritreme is no longer distinct. The spiracular slits lie close together in a light central area surrounded by a broad black heavily chitinized band which has the external scar united with its inner border; whereas in *Myiospila* at this stage (Fig. 106) each spiracular slit has a distinct dark encircling border which renders it more conspicuous. In *Mydaea* the spiracular slits have no such border and their boundaries are therefore rather indefinite. In *Myiospila* the external scar has become obscured by heavy chitinization, while in *Mydaea* it is still fairly distinct. Again in *Myiospila* there are four light areas close to

the outer ends of the spiracular clefts; these seem to correspond with the openings of perispiracular glands, but are not nearly so distinct as in the early 3rd stage.

These openings are not apparent in *Mydaea*, although just below the outer end of the middle slit there is a large round clear opening which is not seen in *Myiospila*.

The fully grown larva is 13 mm. long, slightly larger than that of *Myospila*, but, apart from size and the small spiracular differences, the larvae of these two species are remarkably similar. Similar ventral bands of spines are present on the front borders of abdominal segments I–VII. The position of the spiracular plates on the last abdominal segment and the relative distance between them are the same in each larva (Fig. 96). In *Mydaea urbana* the small size of the posterior spiracles again betrays the fact that the 3rd stage is reached very early in the life history. The ventral surface of the last abdominal segment bears a curved anal plate (Fig. 95) of the usual type.

Buccopharyngeal armature (Fig. 97). The basal piece (*B.*) is like that of *Myiospila* deeply excavate posteriorly, the two lateral plates more approximated than in coprophagous larvae, and running parallel so as to form a firm compact sclerite. What seems to be a constant feature of the basal piece is a conspicuous black heavily chitinized bar which runs midway along each lateral plate parallel to the ventral surface. In the early 3rd stage this bar is continued as the dorsal edge of the ventral cornua, but in the late 3rd stage and in armatures extracted from the puparium, it appears to slope downwards across the ventral cornua owing to that part of the basal piece adding dorsal extensions during the growth of the larva. This bar is absent from the armature of *Myiospila*. The other parts of the buccopharyngeal armature are almost exactly like those of *Myiospila* and are of obvious carnivorous type.

The 2nd stage larvae of *Mydaea urbana* are coprophagous, but the 3rd stage larvae are actively carnivorous. The remarks which have been made about the carnivorism of *Myiospila* apply almost word for word to that of *Mydaea*. The larvae are obligative carnivores and eventually die if deprived of living food; moreover, cannibalism readily occurs if two or more *Mydaea* larvae are present in the same culture, especially during the early 3rd stage, and it is necessary, as in the case of *Myiospila*, to breed each larva separately. The larvae of *Cryptolucilia* form the principal source of food, but larvae of *Haematobia* and *Dasyphora* are equally acceptable. Under similar conditions the larval stage of *Mydaea* was usually found to be longer than that of *Myiospila*. The pupal period in August lasted 22–23 days.

Puparium (Fig. 94)

Since the life history of *M. urbana* up to this point has shown such a remarkably close similarity to that of *Myiospila*, it would be natural to expect that the pupal stages would also be fairly similar. However, this is not found to be the case. There is no silken cocoon formed in *Mydaea*; the surface of the

puparium is rough, and owing to some sticky secretion is closely studded with small earth particles and grains of sand which are firmly adherent to it. A larva which has pupated in the soil can easily be mistaken for a small lump of earth, just as in the case of *Muscina pabulorum*. There is, however, this important difference between those two types, that the earthen cocoon of *Muscina* encloses the puparium but does not adhere firmly to it, while in *Mydaea* there is no silk-lined cocoon formed, the earth particles being independently fixed on the skin and not being united with each other to form a continuous and coherent enclosing layer. The puparium is 6·5 mm. long and the prothoracic nymphal spiracles (Fig. 139) project, as prominent pupal spiracles, laterally through the earth covering from the hind border of the 1st abdominal segment.

On eclosion the puparium opens in the usual manner.

Hebecnema umbratica Mgn.

The only information we have about this species is due to Portchinsky (1910) whose limited observations, mentioned by Keilin (1917), indicate that the egg is of the same type as *Mydaea* and *Myiospila* and that the larvae are probably carnivorous.

Hebecnema umbratica is a common and widely distributed dung-frequenting anthomyid, but easily escapes notice because of its small size and dull inconspicuous appearance. Males and females can be seen on nearly every dung-cake during summer from June until September, and are most abundant on dung a day or two old.

The ovipositing habits of this fly are very like those of *Mydaea*, the eggs are laid singly over the surface of the dung-cake and are fairly uniformly distributed. Only two or three eggs may be laid on each cake by a female, but I have seen as many as nine laid within 20 min., and the total number of eggs is probably much greater than this.

The egg (Fig. 153) is almost identical with that of *M. urbana* in form and appearance. It is much smaller however, being 1·5 mm. long, but it has the same three-horned appearance due to the well-developed lateral flanges being produced anteriorly into diverging pointed processes, and to the presence of a pointed median process. The distance between the tips of the two lateral processes is 0·5 mm. The dorsal strip is similarly flattened while the ventral surface is convex. The egg is laid in such a way that the anterior 3-horned end projects above the surface of the dung, and examination of dung-cakes 2 or 3 days' old usually reveals numbers of those conspicuous eggs.

The only other egg laid in cow-dung which might be mistaken for that of *Hebecnema* is the egg of *Scatophaga* which is laid in a similar position and at first sight also appears to be 3-horned. The middle process, however, is shorter than the lateral processes and ends bluntly, while the two lateral processes, if traced inwards, are found to meet a little behind the front end and are not continued as lateral flanges.

Eggs of *Hebecnema*, under normal conditions, hatched 46 hours after they were laid; in very warm weather, however, this time was reduced to 26 hours. On hatching, the dorsal strip is raised up like that of *Myiospila* or *Mydaea*, and falls back into place after the larvae have emerged. The newly hatched larva was in every case in the 2nd stage.

2nd stage larva (Fig. 88)

Here, as in the case of *Myiospila* and *Mydaea urbana*, I have considered it to be the 1st stage which is omitted from the life cycle and not the 2nd stage as Portchinsky thought.

The newly hatched larva is amphipneustic; the anterior spiracles on the prothorax are 4-lobed, while the posterior spiracles project markedly backwards from the end of the body and are heavily chitinized. Each of them opens by a single aperture on the sloping face and they are, as in *Myiospila* and *Mydaea*, typical 1st stage spiracles. Well-marked ventral bands of spines are present on the anterior borders of abdominal segments II–VII.

Buccopharyngeal armature (Fig. 91). The basal piece (*B.*) is like that of *M. urbana* in that there is no vestige of an anterior dorsal bridge. The ventral cornua are longer than the dorsal cornua, and the whole sclerite is not heavily chitinized.

The intermediate piece (*M.*) is well developed and has two elongated lateral plates. The lateral hooks (*l.h.*) are closely apposed except at the base where they curve downwards separately. They are also slightly curved ventrally at the tips. Lying ventral to the hooks are the paired 2nd stage labiate sclerites (*l.sc.*).

As in *Mydaea urbana* and *Myiospila*, so also in *Hebecnema* there is only one ecdysis in the larval stage, when the 2nd stage larva changes to the 3rd stage.

In one instance this change was found to occur within 8 hours after hatching, while in another case the larva did not moult till between 25 and 26½ hours after hatching. The 2nd stage larva is coprophagous, and the brown, coiled, dung-filled gut is easily visible. The larva is 2 mm. long at the beginning of the 3rd stage.

3rd stage larva (Fig. 89)

The 3rd stage larva is amphipneustic and the anterior spiracles have 4 lobes on each side. The posterior spiracles (Fig. 137) have three elongate oval radiating slits on each side very like those of the early 3rd stage *Mydaea urbana*. In the fully grown larva the peritreme is still distinct since the spiracular plates have not become heavily chitinized. The four round openings of perispiracular glands (*ps.gl.*) are unusually large, and in association with each of them are branched radiating palmate hairs (*pal.h.*). Ventral spine bands are present on the front borders of abdominal segments II–VII, and the last five of these are especially prominent. On the anterior border of the ventral surface of the last abdominal segment is a small but distinct anal plate (Fig. 92)

of usual shape. The head (Fig. 93) is deeply divided by a median fissure into two head lobes, each of which bears an antenna (*ant.*) and a maxillary palp (*mx.p.*). The paired labial palps (*l.p.*) are more easily seen here than in *Mydaea*.

Buccopharyngeal armature (Fig. 93). The basal piece (*B.*) is less strongly chitinized than in *Mydaea*, and differs in having a more prominent anterior dorsal bridge (*d.b.*) from which the dorsal surface runs in a straight line to the blunt tips of the slightly divergent dorsal cornua (*d.c.*).

The ventral surface of the basal piece is also more rounded or convex in side view than in *Mydaea*. The intermediate piece (*M.*) is of the normal carnivorous type and seems to be connected to the anterior dorsal bridge by a light median expansion. The lateral hooks (*l.h.*) and the complete median ventral arch (*m.v.a.*) are of the usual carnivorous type. The accessory sclerites are a pair of oral bars (*o.b.*) posteriorly, and a pair of anterior rods (*a.r.*) which curve upwards beyond the tips of the lateral hooks.

Experiments and observations on the 3rd stage larvae have shown that Portchinsky was justified in suspecting them of carnivorism.

From the carnivorous type of buccopharyngeal armature and from the similarity of the life history to that of *Myiospila* and *Mydaea urbana* we would expect, and we find, a similarity of larval habits. The 3rd stage larvae of *Hebecnema* are obligative carnivores; various coprophagous larvae introduced were attacked and devoured and I have been unable to breed *Hebecnema* larvae to maturity on pure dung.

The amount of living food consumed is naturally much less than in the case of *Myiospila* or *Mydaea*. The full-grown 3rd stage larva of *Hebecnema* is only 6 mm. long, yet one larva during its entire 3rd stage consumed 16 *Cryptolucilia* larvae, and another one ate 20 *Cryptolucilia* larvae of correspondingly similar size, taken from a parallel culture. Another *Hebecnema* larva entirely consumed three, and partly devoured two, similar-sized *Cryptolucilia* larvae in 10 hours.

The full-grown larva is yellowish with small black posterior spiracles, it pupates in the dried dung and the pupal period in August was found to last 15 days.

Puparium (Fig. 101)

The puparium is 4 mm. long, light brown in colour, and distinctly waisted between the 1st and 2nd abdominal segments. The prothoracic nymphal spiracles (Fig. 103) are very large and conspicuous, and project dorso-laterally from the hind border of the 1st abdominal segment.

The anterior segments form a rounded knob and on the last abdominal segment are visible the posterior spiracles, and ventrally the anal plate, of the larva.

The puparium opens in the usual way by means of a circular split round the 1st abdominal segment and by a transverse split round the anterior end.

Mydaea pagana Fabr.

Up till the present time no observations seem to have been made on the biology and early stages of this anthomyid. *Mydaea pagana* is only occasionally seen in Ayrshire although it is more frequent in the island of Arran. In general appearance it is very like *M. urbana*, but in the field its orange scutellum contrasts with the grey scutellum of that fly.

At Brodick in Arran during September, *M. pagana* was seen several times on cow-dung in the fields, frequently accompanied by *M. urbana*. The female lays many eggs scattered singly over the surface of fairly fresh dung-cakes. The eggs, of characteristic form, are embedded in the dung with the anterior end exposed, in the same way as those of *M. urbana*, and are easily seen without disturbing the dung. In one case about three dozen eggs were found distributed over several dung-cakes lying close together, and in another case, at the end of September, forty eggs were taken from a single dung-cake. The female evidently lays most or all of its eggs at one time, and there is no particular preference for freshly dropped dung.

The egg (Fig. 151) is different from any other found in cow-dung. It is 2·5 mm. long and has two prominent parallel lateral flanges which are produced forwards as curved processes. There is no medial anterior pointed process like that of *M. urbana* and in its place is a short blunt medial lobe which is rounded and not serrate. The dorsal surface between the flanges is flattened while the ventral surface is convex. On hatching, the flat dorsal strip, with its edges formed by the lateral flanges, lifts up anteriorly just as it does in the egg of *Myiospila* and *Mydaea urbana*, to fall back into place when the newly hatched larva has crawled free. Eggs laid in the middle of the month took 72 hours to hatch at fairly low temperatures. At the end of the month eggs took over 3 days to hatch.

The most outstanding feature of the life history is that the larva on emerging from the egg is already in the 3rd stage (Fig. 99).

On several occasions eggs were watched during the process of hatching and in each case the larva which emerged was amphipneustic with three posterior spiracular slits on each side, and had the complete 3rd stage buccopharyngeal armature with no indications of any earlier stage structures or exuvia. If there was any relation between the life history of this species and that of *M. urbana*, we would naturally expect to find some relics or vestiges of earlier stages, either in the larva before hatching or within the empty egg after eclosion. All the eggs from which the 3rd stage larvae had hatched were examined and in every case they contained, within the usual vitelline membrane, the greatly reduced but still recognizable exuvium of the 2nd stage larva. A larva extracted prematurely from the egg was found to be enclosed loosely in this 2nd stage cuticle; this exuvium was shed at once and the larva, now in the 3rd stage, crawled actively away. *Mydaea pagana* therefore resembles *M. urbana* and *Myiospila* in having only two larval stages separated by a single moult,

but differs from them in that the first of these stages is spent within the egg and the single ecdysis in the larval stage is coincident with hatching, the 3rd stage larva alone having a free external existence.

The exuvium of the 2nd stage larva extracted from the egg is greatly reduced (Fig. 98) but it still contains recognizable structures which are sufficient in themselves to indicate to which stage this larva belongs.

There is a pair of anterior spiracles (*a.sp.*) which are 4–5-lobed. The posterior spiracles (*p.sp.*) are evidently of a 1st stage type and have branched palmate hairs radiating from their tips. The buccopharyngeal armature (Fig. 98), as might be expected, is greatly reduced. The component parts in themselves are not immediately recognizable, but from their arrangement and relation to each other they can be correlated with the parts of the 2nd stage skeleton of *M. urbana*. The basal piece (*B.*) (Fig. 105) has almost entirely disappeared, all that remains being a pair of faint bars or strands. The middle piece (*M.*) is not so reduced and has its two lateral plates still evident. Anteriorly there are two pairs of sclerites of which one pair is well developed and probably corresponds to the lateral hooks (*l.h.*) while the other pair is weakly developed and may possibly be equivalent to the labiate sclerites (*l.sc.*) of *M. urbana*. In addition there is a relatively large and massive piece (*sb.t.*) in front of these, consisting of six sharp pointed suprabuccal teeth arising from a conspicuous base which is divided into two by a median cleft. There are apparently five bands of ventral spines, each band with several rows of short irregular spinules.

This exuvium, despite the reduced nature of the skeleton, is evidently that of a 2nd stage larva and differs from the *M. urbana* type mainly in the possession of the suprabuccal teeth which are also of interest in that they are absent and unrepresented in the 3rd stage.

3rd stage larva

The newly hatched larva is about 3 mm. long and is in the 3rd stage. The anterior spiracles (Fig. 100) are 4-lobed; the posterior spiracles (Fig. 104) project prominently from the posterior face of the last abdominal segment. Each protruding spiracle ends in a strongly chitinized oval plate which bears three irregularly oval spiracular slits radiating from the circular external scar. The peritreme is distinct, but the only indication of perispiracular glands is a single round opening between the outer tips of the middle and lower spiracular slits, rather like that described for *Mydaea urbana*. In the late 3rd stage the spiracles are relatively very small and are heavily chitinized, appearing as paired black projections from the hind end of the larva.

Ventral spine pads are present on the front borders of abdominal segments II–VII, and the ventral surface of the last abdominal segment bears a curved anal plate (Fig. 138). The massive 3rd stage skeleton is visible through the cuticle, and its front part appears as if it is surrounded by a complete dark internal ring. This peculiar feature, which gives the young larva quite a distinctive appearance, is due to the infolding of the anterior spiny border of

the 1st thoracic segment (Fig. 102). The closely set regular rows of spines which are normally directed backwards are now seen to point forwards due to the overfolding of the thoracic segment, and the telescoping has resulted in the basal part of the head becoming covered and concealed.

The paired antennae (*ant.*) are borne on the front of the head, and lying ventral to them are the paired maxillary palps (*mx.p.*).

Buccopharyngeal armature (Fig. 105). In general appearance and arrangement of the parts the skeleton is very like that of *M. urbana*. The basal piece (*B.*) is compact and heavily chitinized, and its lateral plates with the cornua are closely apposed. The lateral plate has no longitudinal thickened bar like that of *M. urbana*. The middle piece (*M.*) articulates very closely with the basal piece behind and with the bases of the lateral hooks in front. Lying ventrally to the strongly curved paired lateral hooks (*l.h.*) are two pairs of accessory sclerites, the oral bars (*o.b.*) extending from the base to the tip of the lateral hooks, and dorsal to these the paired anterior rods (*a.r.*) whose distal ends, furnished with spikes, curve inwards round the front of the lateral hooks. The median ventral arch (*m.v.a.*) forms a strong complete arch.

The armature is of the carnivorous type and the habits of the 3rd stage larvae are very similar to those of *M. urbana*. The larvae not only prey on other dung-frequenting larvae but will also readily attack each other. It was due to this extensive cannibalism, as well as to the difficulty of maintaining the supply of living food, that only two of the many larvae which hatched survived long enough to pupate. Apart from the carnivorous habits, however, the most important feature of this life history is the hatching of a fully developed 3rd stage larva from the egg.

The occurrence of this phenomenon among the Anthomyidae will be more fully discussed when dealing with *Phaonia variegata*.

Two larvae which hatched from eggs laid on 29 September were full-grown and pupated in the earth at the beginning of November—on 10 November in one case. Eclosion has not yet been obtained and one of these puparia, kept under perfectly natural conditions, is still—12 March—in a healthy pupal state.

Puparium (Fig. 135)

The puparium is of the usual anthomyid type and has neither a silken cocoon like *Myiospila* nor a covering of earth particles like *M. urbana*. It is 6·5 mm. long and light brown in colour. The posterior larval spiracles project prominently from the upper part of the last abdominal segment. They are heavily chitinized and the spiracular plan is obscured. On the ventral surface of this segment is a distinct anal plate (Fig. 138) with strongly curved side arms. The prothoracic nymphal spiracles (Fig. 136), like those of most other carnivorous forms, project as prominent pupal horns (Fig. 135, *pu.sp.*) dorso-laterally on the 1st abdominal segment. In front of the border between the 1st and 2nd abdominal segments, the puparium is distinctly waisted. The

method of eclosion has not yet been observed, but a moribund puparium ruptured easily along lines of weakness and the direction corresponded to the normal circular split round the 1st abdominal segment in front of the pupal spiracles, and to the transverse split running forwards from this round the front end of the puparium.

Phaonia (Hyetodesia) variegata Mgn.

Hitherto there have been very few observations on the habits and life history of this species.

Dufour (1839) described a single puparium of this fly found in earth under a mass of *Boletus pinetorum*. Keilin (1917) found the larvae in decaying *B. edulis* and established the fact of their carnivorous habits by finding that they preyed on the larvae of *Pegomyia winthemi* Mgn. which accompanied them, and on the larvae of *P. transversa* Fallen which lived on *Armillaria mellea*. Owing to scarcity of material he had to describe the structure of the larva from the puparium after eclosion and he indicates that the buccopharyngeal armature is of the typical carnivorous type. Each of these authors refers to the prominent pupal spiracles and the method of eclosion.

For three successive years I have been fortunate enough to observe the habits and complete life history of this anthomyid and to have sufficient material to describe the larva in all its stages.

The adult fly is very apt to be confused with the very similar *Phaonia* (*Hyetodesia*) *scutellaris* Fallen. Meade (1897) does not make the distinction between these two species perfectly clear and also says that *Hyetodesia scutellaris* is very common while *H. variegata* is very rare. Wingate (1906) observes that *H. variegata* is the common yellow *Hyetodesia*. Séguy (1923) using the characters of the pre-sutural acrostichal bristles makes the distinction between these two species comparatively simple, and using this feature I find that I have only a single record of *H. scutellaris* compared with numerous records of *H. variegata*. The latter is undoubtedly the commoner fly, although it is never very abundant.

The eggs were first seen on the upper surface of the pileus of *Polyporus* which was growing beside the rotting stump of a beech tree on 29 September, and females were observed ovipositing there. The eggs were laid singly or in groups of two or three on dead leaves and pieces of grass lying on top of the fungus, seldom on the fungus itself and were nearly always exposed. In the following year on 25 September this was observed again on rotting *Polyporus* where the eggs were laid either singly on the fungus or in groups of up to half a dozen on dead leaves lying on the top. The total number of eggs laid by each fly is evidently not large; two females in captivity each laid about 25 eggs on the fungus.

On 5 October the flies were observed ovipositing in damp moss on a tree stump close to a large *Polyporus*. The eggs have never been seen on any other fungus or anywhere else but in its immediate neighbourhood.

The egg (Figs. 118–21) is very characteristic, resembling that of *Graphomyia* in having well-developed lateral flanges. It is about 1·75 mm. long and the anterior end is slightly more tapering than the posterior end.

The flat surface between the flanges is honeycomb-marked with the sculpturing of the chorion (Fig. 120), and the rounded surface has nine or ten longitudinal furrows. The flanges themselves are marked with a network pattern and the free edges are regularly lobed (Fig. 121).

Eggs took 9 days to hatch at a fairly low average temperature of 10° C., and since they do not collapse after eclosion look much the same before and after hatching. Examination of the newly hatched larva reveals the interesting fact that it is already in the 3rd stage. This unusual phenomenon has been verified by each of the following methods:

(1) The newly hatched larva (Figs. 123–8) has the structure of a typical 3rd stage carnivorous larva. It is amphipneustic with three slightly divergent slits in the posterior spiracles, and has a complete 3rd stage buccopharyngeal armature with no traces of 2nd stage structures.

(2) No ecdysis nor any of the phenomena accompanying ecdysis were observed during growth to the full-grown larval state. The only differences between the newly hatched and the adult larva are, firstly, in the relative proportion of the posterior spiracles which form a prominent feature of the former larva but are insignificant in the latter due to the great increase in size of the body, and secondly, in the slightly heavier chitinization of the dorsal surface of the basal piece of the mature larva.

(3) Evidence from the egg itself. If the egg is cleared just prior to eclosion (Figs. 118, 119) the form and position of the unhatched larva within can be made out through the transparent chorion, and it is seen to differ in no way from the newly hatched larva which in turn, as has been noted above, is similar to the full-grown 3rd stage larva.

In this preparation (Fig. 119), and also in many others of a similar nature, the peculiar relation of the unhatched larva to the egg can be appreciated. The flat surface between the flanges in this egg is ventral and the concave striated surface is dorsal, a direct contrast to the condition in the eggs of *Myiospila* and *Mydaea* where the flat surface and the flanges are dorsal. When the empty egg-shell is opened after eclosion the delicate transparent vitelline membrane is found to contain what are undoubtedly the vestiges of an almost completely suppressed and scarcely recognizable exuvium of an earlier larval stage (Fig. 124). All that remains to indicate this are a few chitinous parts of the original early stage buccopharyngeal armature which seem to represent lateral hooks and middle piece together with diverging posterior spiracles. Other ill-defined structures may represent accessory sclerites, but they are all so reduced and modified that it is difficult to interpret them accurately. The number and arrangement of these vestigial pieces were found to vary little in the several eggs examined, and it would seem that this condition in *Hyetodesia variegata* is a further degree of the specialization which occurs in

Mydaea pagana, the suppression of the early stages being even more complete than in that species.

Both *Mydaea pagana* and *Hyetodesia variegata* hatch from the egg as 3rd stage larvae, but in the former case this habit is evidently of more recent acquisition than in the latter since the vestiges of the ancestral mode of life have not been so thoroughly divested.

Three stages in the progressive suppression of the early larval stages are represented by *Myiospila* or *Mydaea urbana*, *Mydaea pagana* and *Hyetodesia variegata*, and fuller knowledge of the early stages of other Anthomyidae, especially those of carnivorous habit, would probably enable a more complete series to be established, culminating possibly in a species whose egg contained no indications of exuvia at all.

The normal hatching of a 3rd stage larva from the egg and the consequent occurrence of only one larval stage is a very rare phenomenon among the Anthomyidae.

So far it has only been observed to occur in four species: in *Melanochelia riparia* Fallen by Keilin (1917), in *Phaonia* (*Hyetodesia*) *variegata* Mgn. and *Mydaea pagana* Fabr. by myself, and recently in *Phaonia mirabilis* Ringdahl by Tate (1935). I am convinced, however, considering how incomplete is our knowledge of the early stages of the great majority of anthomyids, that this phenomenon is far more widespread than is commonly believed. Further investigations of the species of *Phaonia* would very possibly reveal life histories of a similar kind, and I would go so far as to suggest that trimorphism in the larval stage will, with more complete knowledge, be found to be the exception rather than the rule in species of *Phaonia* and *Mydaea*.

Larval habits

The newly hatched larva is about 2·5 mm. long and is in the 3rd stage. It is carnivorous from the time of hatching and never seems to depart from this mode of life. The *Polyporus* fungus is usually fully grown early in August and remains in this condition for nearly two months, but by the end of September it is normally riddled with fully grown Mycetophilid larvae which form the basic food supply of the *Phaonia* larvae. From the time of hatching up till the time when it is full grown, the larva seizes and devours large numbers of the soft fleshy larvae of the fungus midge, in this case almost exclusively *Mycetophila ornata* Steph. Other larvae which occur in *Polyporus* are those of *Fannia* which are not preyed on, and those of *Trichocera* which are attacked but are evidently not attractive. By following the life history in the field it is found that the *Mycetophila* larvae are most plentiful about the time when the *Phaonia* larvae are normally hatching, decreasing considerably in numbers during October.

The larva of *Phaonia* is under normal conditions full grown in less than a fortnight, and in this state it spends the winter in a more or less inactive condition either in or underneath the rotting fungus. The larvae which are

smooth, white and from 13–14 mm. long, may be found here and in the earth at any time up till the end of the year. They were found to pupate in January or February, and after a pupal period which varied from 8 to 11 weeks emerged as adults in the third and fourth week of March. Other batches of larvae taken in the field during winter did not produce flies till the fourth week of April.

3rd stage larva (Figs. 122, 123, 125–8)

The fully grown larva has the usual smooth elongated form of the typical carnivorous anthomyid larva. It is amphipneustic and the anterior spiracles have 4–5 lobes on each side. The posterior spiracles (Figs. 123, 125), as has already been noted, are very small inconspicuous black dots in the late 3rd stage and are borne on the tip of small heavily chitinized projecting horns on the rounded posterior face of the last abdominal segment (Fig. 128). In the early 3rd stage they project in a similar fashion but are only lightly chitinized. Each spiracular plate has three radiating spiracular slits like those of *Myiospila* and *Mydaea*, and three small openings of perispiracular glands (*ps.gl.*). The anterior border of the 1st thoracic segment (Fig. 122) has about a dozen closely set rows of short sharp recurved spines, and ventral bands of spines are also present on the anterior borders of abdominal segments I–VIII. These are better developed and more conspicuous towards the hind part of the body. The ventral surface of the last abdominal segment bears an anal plate of the usual type.

The head (Fig. 122) is specially well developed in this larva. From round the mouth a series of large branching oral grooves (*or.gr.*) spreads forwards and upwards. Near the origin of these grooves are the paired labial palps (*l.p.*). The paired antennae (*ant.*) and maxillary palps (*mx.p.*) borne on the front part of the head are seen to be continued internally as paired tubular sacs. On the ventral surface between the labial palps and the maxillary palps is another pair of sensory organs (*C.*) each with a tubular papilla on a rounded lobe; these correspond to sensory organs (*C.*) (Keilin, 1915). Above the maxillary palps and medial to them is a fifth pair of sensory organs (*s.o.*).

The buccopharyngeal armature (Figs. 126, 127) is of a distinctly carnivorous type but is worthy of special notice in the ways in which it differs from the typical *Mydaea-Myiospila* arrangement. The basal piece (*B.*) is compactly formed with a projecting anterior dorsal bridge (*d.b.*). The middle piece (*M.*) is massive and of rather unusual form with a lighter median dorsal expansion. The common salivary duct (*sl.d.*) which terminates in this piece is of unusually large calibre. The paired lateral hooks (*l.h.*) are large, strongly curved and sharply pointed. They are very closely apposed appearing like a single claw in side view, but a dorsal view (Fig. 126) clearly shows their paired structure. Projecting forwards from the massive bases of the lateral hooks is a pair of stout rods (*ob.+a.r.*) which run parallel to the tip of the hooks, bending inwards and uniting in front of them. The posterior part of these rods is probably equivalent to the oral bars (baguettes orales of Keilin), and the

anterior part to the anterior rods or ribbons (ruban antérieur of Keilin) of other carnivorous larvae. Each of these stout rods gives off ventrally a curved posterior ribbon (*po.r.*) which bends back and runs parallel to them as far as the median ventral arch. Between the stout rods and the concave under-surface of the lateral hooks is a lightly chitinized strip (*d.st.*) which is quite isolated and has apparently no connexion with the other sclerites. The median ventral arch (*m.v.a.*) is well developed and, as in other carnivorous types, is in the form of a complete, uniformly heavily chitinized arch.

The complete length of the late 3rd stage skeleton is one-third more than that of the newly hatched larva, as compared with the length of the larva itself which is six times greater.

Puparium (Figs. 112–14)

The light brown puparium is 7 mm. long with a greatest breadth of 3 mm. The prothoracic nymphal spiracles (Fig. 113) project laterally as conspicuous pupal horns near the hind margin of the 1st abdominal segment.

The rounded posterior face of the last abdominal segment is marked with a curious network of branching ridges; on the ventral surface of this segment is a distinct and detachable anal plate. On eclosion the puparium opens in the usual manner.

Muscina pabulorum Fallen

The accumulated information about this anthomyid has been summarized by Keilin (1917) and consists briefly of the following observations. Ratzeburg (1844) obtained it several times from *Bombyx pini* and *B. monacha*. Beling (1868) found that the migratory larvae of *Sciara militaris* Now. are always accompanied by those of *Muscina pabulorum*. Furthermore, the larvae of *Muscina* destroy the bodies of larvae and nymphs of *Sciara* and also attack them when alive. Similar observations, which are mentioned in his work, have been made by other authors.

Verhoeff (1891) raised a large number as parasites of *Bombus agrorum*. The formation of the cocoon by the larva has been described by Keilin (1919).

These observations indicate the carnivorous tendencies of the larva, but up till the present time we have no precise details about the degree and extent of this carnivorism and no information either about the ovipositing habits of the female or about the life history and larval morphology.

Muscina pabulorum is not an uncommon fly, but the numbers seen vary very greatly from year to year. For example, in 1935 not a single specimen was seen in the field throughout the whole year. I find that this fly is an occasional visitor to carrion and the only places where I have seen the gravid females are on dead birds and fish heads left exposed outside as bait, and on a barrel full of dead hens in a farmyard. Carrion in the later stages, when it is already partly consumed by larvae of *Calliphora*, *Lucilia*, and *Hydrotaea*, is specially attractive, not only to *Muscina pabulorum* but also to *M. stabulans*,

but in the case of the latter species I have never been able to observe or induce oviposition on this substance.

Gravid females of *M. pabulorum* put in with the carrion which originally attracted them soon start ovipositing. Each female may lay only a few eggs but usually the number is quite large, and in one case 60 and in another case 150 eggs were laid.

The egg (Fig. 142) is 1·5 mm. long and has well-developed lateral flanges like that of *Graphomyia* and *Phaonia variegata*. The flanges are well separated and the surface between them is flattened and honeycomb-marked. The other more extensive surface is convex and has about ten well-marked longitudinal corrugations. A very similar type of egg has been described for *Muscina stabulans* by Portchinsky (1913) and for *M. assimilis* by Keilin (1917). In those species the flat surface of the egg is described as dorsal and the convex surface as ventral. This type of egg, however, is very like that of *Phaonia variegata* in which I have found the flat surface to be ventral (Fig. 119). Only an examination of the egg just prior to hatching can decide this point; and although I have not been able to do this in the case of *Muscina pabulorum*, I regard the flat surface between the flanges as ventral and not dorsal. The length of the egg stage seems to vary a great deal; in one case a batch of eggs took 66 hours to hatch and in another they hatched 36–38 hours after being laid.

The newly hatched larvae were in every case in the 1st stage.

1*st stage larva*

The newly hatched larva is metapneustic. The posterior spiracles, which are situated on the dorsal part of the posterior face of the last abdominal segment, are not heavily chitinized but they project farther than in most other 1st stage larvae. The larva is very slender, tapering gradually towards the anterior end. Ventral spine bands occur on the anterior borders of abdominal segments II–VII. On the ventral surface of the last abdominal segment is the anal plate which is not so distinct as usual, and scattered spines are present without forming a distinct band. A few weakly developed spinules are present on the front border of the prothorax. The head (Fig. 131) has well-developed paired antennae (*ant.*) and maxillary palps (*mx.p.*), and is bilobed in front.

Buccopharyngeal armature (Fig. 131). The basal piece (*B.*) is of the usual 1st stage form; it is uniformly heavily chitinized and a complete but slender anterior dorsal bridge (*d.b.*) is present. The basal piece is produced anteriorly into a pair of long slender arms which embrace terminally the 1st stage middle piece (*m.*). The median dorsal sclerite (*m.d.s.*) is blade-like, and its base is in close relation with the front of the middle piece. Lying ventrally are the two curved *t*-pieces (*t.sc.*) and immediately in front of their closely apposed tips is a pair of triangular suprabuccal teeth (*sb.t.*). I have no exact information about the length of the 1st stadium; but of two separate batches of larvae

examined 24 hours after hatching, one still consisted of 1st stage larvae while those of the other had all attained the 2nd stage.

2nd stage larva

The 2nd stage larva is amphipneustic. The prothoracic spiracles have 5 lobes on each side and the posterior spiracles (Fig. 132), no longer projecting, have two pear-shaped spiracular slits in each plate. The arrangement of spines on the body segments is very like that of the 1st stage larva. At the beginning of this stage the larva is about 4 mm. long.

Buccopharyngeal armature (Fig. 134). The basal piece (*B.*) is well developed with prominent dorsal and ventral cornua. The anterior dorsal bridge (*d.b.*) is complete and reticulate.

The middle piece (*M.*) consists of elongate lateral plates joined ventrally by a transverse arch. From the front border of the middle piece a pair of slender sclerites run forward to the base of the lateral hooks (*l.h.*) which are separated proximally but closely apposed distally. Ventral to the latter are the paired labiate sclerites (*l.sc.*) and a pair of accessory pieces (*a.sc.*). Beyond the tips of the lateral hooks are two triangular suprabuccal teeth (*sb.t.*).

The head (Fig. 134) with its paired antennae (*ant.*) and maxillary palps is bilobed anteriorly and ventrally, and from the mouth opening numerous fine oral grooves radiate outwards and upwards.

3rd stage larva

The 3rd stage larva is amphipneustic and the anterior spiracles have 5–7 lobes on each side.

The posterior spiracles (Figs. 109, 110) are of the typical *Muscina* type but there is a considerable difference between those of the early and late 3rd stage. In the early 3rd stage (Fig. 109) the peritreme is complete and distinct and is expanded on the inner border of the spiracular plate to include the external scar. The three spiracular slits are sausage-shaped and have numerous inwardly projecting teeth round the edges. They radiate out from a point about midway between the external scar and the centre of the plate. In the late 3rd stage (Fig. 110) the spiracular plates have become heavily chitinized, the peritreme and external scar are no longer distinct and the spiracular clefts have shortened considerably so as to be more pear-shaped. Between the two upper slits or clefts is a clear triangular area of large size. In the full-grown larva the spiracular plates are separated by a little less than half their breadth.

The last abdominal segment is smoothly rounded posteriorly and bears ventrally an anal plate of normal form; behind this the ventral border of the segment is broken up into several prominent post-anal lobes. Ventral spine pads are present on the front borders of abdominal segments II–VII. The head (Fig. 129) has numerous oral grooves radiating from its ventral surface and it bears paired antennae (*ant.*), maxillary palps (*mx.p.*) and labial palps (*l.p.*).

Buccopharyngeal armature (Fig. 129). The basal piece (*B.*) is very like that of *M. assimilis* Fall. described and figured by Keilin (1917). It is not uniformly chitinized, the anterior dorsal bridge is not prominent and the ventral surface is marked by a series of longitudinal pharyngeal ridges connected by short transverse ridges. The middle piece (*M.*) is strongly developed and heavily chitinized; it receives ventrally the terminal part of the common salivary duct (*sl.d.*).

The lateral hooks (*l.h.*) are equal and closely approximated. They are strongly curved and each massive base has a clear round, more lightly chitinized, area. The median ventral arch (*m.v.a.*) forms a complete continuous arch. The accessory sclerites consist of a pair of oral bars (*o.b.*) with peculiar basal enlargements, and what appears to be a pair of anterior rods (*a.r.*) but which may possibly be only a dorsal expansion of the oral bars. Below the tip of the lateral hooks is a row of six backwardly directed suprabuccal teeth (*sb.t.*, Fig. 130). The teeth are set closely together, but the series is divided into two by a median gap.

The larva in the 1st and 2nd stage is purely saprophagous; like the larvae of *Calliphora* and *Lucilia* it feeds on the decaying carrion and even in the absence of its normal food it is not attracted to living prey. In the 3rd stage, however, the larva becomes a facultative carnivore capable of attacking and devouring other carrion-frequenting larvae. Larvae of *Muscina pabulorum* can be reared from egg to adult on dead meat alone, spending the whole larval stage as purely saprophagous types; under these conditions development is in no way retarded and they may be full grown and ready to pupate 7 days after hatching.

On the other hand, larvae of *Calliphora* or *Lucilia* introduced were seized and devoured in true carnivorous fashion, irrespective of size. The carnivorism is not so thorough as in the case of *Myiospila*, and larvae took more time to completely demolish their prey.

These observations are therefore in accordance with those of the authorities mentioned above, since they indicate that the 3rd stage larvae of *Muscina pabulorum* are semi-carnivorous or facultative carnivores which thrive equally well on dead decaying material and on living prey.

The nature of the buccopharyngeal armature alone would point to this conclusion. As in *Mesembrina meridiana*, the basal piece is of the saprophagous type; it is not nearly so compact and heavily chitinized as that of a true carnivore, and it bears ventral pharyngeal ridges. On the other hand, the carnivorous capabilities are betrayed by the nature of the lateral hooks, by the presence of well-developed accessory sclerites and suprabuccal teeth, and by the median ventral arch being complete and not in the form of separate dental sclerites.

The fully grown larva of *Muscina pabulorum* is 15 mm. long, smooth, white and plump, and has the very unusual habit of constructing a compact cocoon of foreign material in which pupation takes place. Keilin (1919) has given a

short account of the formation of the cocoon as observed by G. S. Graham-Smith and J. E. Collin. The larvae, which were bred on a dead guinea-pig, when fully grown formed cocoons made of the animal's hair, and in the case of *M. stabulans* these observers noticed that earthen cocoons were formed. In my experiments with the larvae of *M. pabulorum* I have always found that when they are fully grown they leave the carrion on which they were breeding and go into the earth. On examining the earth a few days after, there was no sign of prepupal larvae or of puparia, but there were several small, roughly equal, oval masses of earth very liable to be overlooked. These were the earthen cocoons formed by the larvae before pupation. When there is a relatively large amount of earth the earthen cocoons are quite isolated, but when a large number of larvae is put into a small amount of earth, a solid flat cake of earth, studded with closely packed vertical puparia, is formed.

The puparia are actually in contact with each other while the spaces left between are cemented up with coherent earth particles. The whole compound structure appears rather like a honeycomb. A typical isolated cocoon, on the other hand (Fig. 115), is oval in shape, about 12 mm. long, usually made of small earth particles, and while the outside is rough and irregular, the inner surface in contact with the puparium is smooth and glistening in appearance. This lining is evidently formed by a sticky larval secretion which also cements the grains together. A fully grown larva, however, put between clean watch-glasses, pupated like any normal anthomyid and, in contrast to the behaviour of *Myiospila* under the same conditions, it did not form a silken cocoon. Possibly the sticky secretion is only produced in the presence of foreign particles of earth, fur, or other material suitable for a cocoon.

Puparium (Fig. 116)

The puparium is usually about 9 mm. long and squat in form with both ends more bluntly rounded than in most other anthomyids. The last segment bears the larval posterior spiracles and a distinct anal plate. The prothoracic nymphal spiracles (Fig. 117) project as pupal horns or pupal spiracles dorso-laterally near the hind margin of the 1st abdominal segment. The intrapupal spiracles (*in.p.s.*) are well developed and have a more definite pattern than usual of circular papillae.

On eclosion the puparium opens by a circular split round the 1st abdominal segment just in front of the pupal spiracles and by a transverse anterior slit. The pupal period was found to last usually about 3 weeks.

From my observations it would seem that *Muscina pabulorum* normally breeds on carrion, and in this respect it is interesting to note that on three occasions I have taken larvae from living sheep along with other sheep maggots. The occurrence of this species as an occasional myiasis-producing fly is not altogether surprising when we consider that many Calliphorines which normally breed on carrion have recently shown an increasing tendency to adopt a parasitic mode of life as sheep maggot flies. Moreover, the closely related

M. stabulans has been recorded on many occasions by different observers as a myiasis producer. On carrion, the larvae of *M. pabulorum* are semi-carnivorous and it is interesting to speculate whether in this new habitat they behave as harmful parasites of the sheep, or whether they are really beneficial, preying on other sheep maggots. Suitable opportunities for deciding this point have not yet arisen, but the probability is that they feed, not on other larvae but on the skin products and tissues of the living sheep.

Summary and discussion

I. *The egg*

A survey of the relatively few anthomyid types described in this paper alone is sufficient to show that the external form of the egg may differ greatly from species to species. It would be interesting to find out if these differences are related in any way to the subsequent development or habits of the larvae. The eggs of the higher Anthomyidae which I have examined may be placed in the following three groups:

(1) The *Musca* type. Cylindrical, oval, with the dorsal surface slightly concave and the ventral surface convex. The parallel dorsal ribs, usually faint, are separated by a narrow strip and never project as flanges. No outgrowths of the chorion are present. Belonging to this group are the following: *Musca domestica*, *Stomoxys calcitrans*, *Cryptolucilia cornicina*, *Dasyphora cyanella*, *Mesembrina meridiana*, *Morellia simplex*, *Polietes hirticrura* and *P. lardaria*. Apart from size and the way they are laid, the eggs of these species differ only from each other in minor details such as the breadth of the dorsal strip and the sculpturing of the chorion. I can find no reliable feature, for example, to distinguish between the eggs of *Morellia simplex*, *Dasyphora cyanella* and *Cryptolucilia cornicina*, which are all laid in very similar batches in cow-dung. With the exception of *Polietes*, all these eggs are laid on or in the medium in which the larvae develop.

(2) The *Myiospila* type. In this type the chorion has extended as paired dorsal flanges which run roughly parallel most of their length, but gradually diverge in their course towards the anterior end where they become more divergent and project forwards as pointed processes. These flanges form the lateral borders of a flat dorsal strip, the front part of which opens like a trap-door on eclosion of the larva. There may also be a median process projecting forwards from the front of the egg. To this group belong *Myiospila*, *Mydaea urbana*, *Hebecnema umbratica* and *Mydaea pagana*. The eggs of these four species are all laid singly embedded in the surface of the dung, frequently with part of the dorsal surface left exposed. These eggs may be laid in this situation in order to reap the full benefit of direct exposure to the sun's rays, and thus to hasten the hatching of the larvae. These species are all obligative carnivores, and it is obviously an advantage for them to reach the carnivorous 3rd stage about the time the saprophagous larvae in the dung-cake are just hatching.

The larval development and habits of these four species are remarkably similar. Instead of the normal trimorphic larva, there are only two larval stages separated by a single moult. *Mydaea pagana* differs only in degree from the others in that the single moult is coincident with hatching of the larva.

(3) The *Phaonia* type. In this type of egg the broad flanges are widely separated and run strictly parallel to each other throughout their length. These flanges are not produced into processes anteriorly but are equally developed at each end. The surface between the flanges is flat while the other convex surface is usually marked with longitudinal corrugations. So far I have found this type of egg only in three species: *Muscina pabulorum*, *Phaonia variegata* and *Graphomyia maculata*, but I have reason to believe that it is also found in other species of *Phaonia*. I have pointed out that the flat surface between the flanges, which in the *Myiospila* type is dorsal, is ventral in *Phaonia variegata*. I have yet to find out if that is a constant feature of this type of egg. The broad flanges of the egg may possibly serve either for attachment to a solid substratum or for supporting the egg the right way up in a very fluid medium.

II. *The buccopharyngeal armature*

1st stage larva. In the 1st stage larva the armature shows greater uniformity of structure than in any other stage. All the 1st stage anthomyid larvae examined possess the characteristic median dorsal sclerite, homologous with the labrum (Keilin, 1915), and the paired *t*-pieces homologous with the labium. In the 1st stage larvae of the semi-carnivorous species, *Mesembrina meridiana* and *Polietes hirticrura*, there is an additional pair of pieces, lying external and ventral to the *t*-pieces, forming the lateral borders of a tongue-like sclerite, especially well marked in *Mesembrina*. In *Muscina pabulorum* there is a pair of suprabuccal teeth and in *Hylemyia* an additional pair of connecting pieces between the tips of the median dorsal sclerite and the *t*-pieces. Another characteristic feature of the skeleton at this stage is the nature of the basal piece. This sclerite is never massive and it always has a conspicuous dorsal bridge and long anterior prolongations which embrace distally the 1st stage middle piece. The larvae of *Stomoxys* and *Haematobia* can be distinguished from those of *Musca*, *Morellia*, *Cryptolucilia* and *Dasyphora*, in having the dorsal cornua of the basal piece well separated from the dorsal bridge by elongation of the main part of the sclerite. In all the purely carnivorous forms or obligative carnivores which I have studied the 1st stage has been omitted from the life history.

2nd stage larva. In contrast to the 1st stage the armature of the 2nd stage shows a great variety of form and construction. Very little attention has been paid to this stage by other authors, and as a result I have been forced, for the sake of convenience, to elaborate new names for some of these structures

which are liable to occur in different species. To a pair of sclerites lying ventral to the proximal half of the 2nd stage lateral hooks I have given the name of labiate sclerites, owing to their front borders forming a sort of lip. These sclerites are frequently closely apposed ventrally, and together form a gutter or spout on the floor of the buccal cavity. They are present in the 2nd stage larvae of *Cryptolucilia*, *Dasyphora*, *Mesembrina*, *Muscina*, *Morellia* and *Polietes hirticrura*, and have been described by previous authors in *Ophyra leucostoma* Weid (Keilin & Tate, 1930) and *Musca domestica* (Patton & Evans, 1929). In *Haematobia* they are doubtfully present. In the atypical 2nd stage larvae of carnivorous forms such as *Myiospila*, *Hebecnema* and *Mydaea urbana* they are present in modified form being especially large and elongated in *Mydaea urbana*. Another pair of peculiar sclerites, found in the 2nd stage alone, are those which I have called the angular sclerites. They lie between the front of the middle piece and the base of the lateral hooks. They are well developed in *Cryptolucilia*, *Dasyphora*, *Morellia*, *Musca* and *Polietes hirticrura*. They are present in modified form in *Haematobia*, but are absent from *Mesembrina*, *Muscina* and the carnivorous forms *Mydaea*, *Myiospila* and *Hebecnema*.

The 2nd stage larva of *Morellia* differs from all others examined in having the closely apposed lateral hooks curved upwards at the tip instead of downwards towards the mouth. The arrangement of the buccal pieces in *Haematobia* seems to bear no relation to that of other related species, but this may possibly be due to a great reduction of the lateral hooks and modification of the labiate sclerites. The homology of the 2nd stage sclerites is, however, very doubtful, and a great deal more work will have to be done before we can compare and correlate these sclerites with certainty. The larva of *Hylemyia* differs from all those of the higher anthomyids described in having the large lateral hooks widely separated and capable of independent movement.

3rd stage larva. The general characters of the 3rd stage anthomyid armature have been so thoroughly discussed by Keilin, especially in relation to habit, that it only remains to mention a few new points, and to emphasize some old ones, whose importance could only be fully appreciated by a study of several saprophagous forms. From my observations on larvae of all three types, saprophagous, semi-carnivorous and carnivorous, I find that the structure of the median ventral arch is of the highest importance in indicating the habits of the larva. In all carnivorous forms such as *Phaonia*, *Mydaea*, *Myiospila* and *Hebecnema*, and semi-carnivorous forms such as *Mesembrina*, *Muscina* and *Polietes hirticrura*, this sclerite is in the form of a complete, compact, and usually uniformly heavily chitinized arch.

In all purely saprophagous forms, on the other hand, such as *Musca*, *Stomoxys*, *Morellia*, *Cryptolucilia*, *Dasyphora*, *Haematobia*, and also *Hylemyia*, this sclerite takes the form of two quite separate, triangular plates which are unconnected ventrally. For these separate sclerites I have retained the original name of dental sclerites given by Hewitt (1914). It might be mentioned

in passing that in the Calliphorinae such as *Lucilia*, *Calliphora* and *Protophormia*, this paired condition of dental sclerites is also found.

Keilin (1915) has shown that the ventral surface of the basal piece is marked with a series of longitudinal pharyngeal ridges in all saprophagous anthomyid larvae, and that these ridges are absent from the pharynx of carnivorous forms. It might be thought that in semi-carnivorous forms these ridges would show a degree of development roughly midway between those two extremes. This is not found to be the case; the ventral surface of the basal piece bears distinct longitudinal ridges in the semi-carnivorous larvae of *Mesembrina*, *Polietes hirticrura* and *Muscina*. A comparison of sections cut through the pharynx of the 3rd stage larvae of *Mesembrina* and the purely saprophagous *Morellia*, for example, shows that the ridges are equally large and well developed in both these types.

In the accounts of the separate anthomyids I have shown how the form and construction of the skeleton can frequently be used as a valuable diagnostic feature. In the present paper I do not intend to discuss the subject in more detail. Although many interesting and suggestive points have emerged I propose to postpone a survey of this materal till a wider and more representative investigation of anthomyid larvae has been carried out.

III. *General characters of coprophagous and carnivorous larvae*

Keilin (1917) has surveyed the morphological characters of carnivorous anthomyid larvae, and to his account I will add a brief description of the relation between the course of larval development and the habits of the larva. All the coprophagous and semi-carnivorous forms which I have studied are trimorphic, passing normally through three larval stages. Even when exceptionally large eggs are laid as in *Mesembrina* the emerging larva is in the 1st stage as also is the viviparously produced larva of *Hylemyia*. In all the purely carnivorous forms, on the other hand, there is a tendency to reduce the number and length of the early stages, so that in *Myiospila*, *Hebecnema*, *Mydaea urbana* and *M. pagana* there are only two larval stages separated by a single moult and the 1st stage has been dispensed with. The early stages may be so reduced that the larva on hatching from the egg is already in the carnivorous 3rd stage as in *M. pagana* and *Phaonia variegata*. Since the 3rd stage structures are assumed at an early stage in larval development, the relative proportions of these structures in the full-grown larva are much less than in the trimorphic larvae. Carnivorous larvae can frequently be distinguished by the very small size of the posterior spiracles, and this character is found useful in the field for separating the carnivorous forms from the otherwise very similar saprophagous members of the community. Another character of less importance is the number of lobes in the anterior spiracles. This number is always small in obligative carnivores, seldom more than 5 lobes on each side and never less than 4. In coprophagous and semi-carnivorous

larvae 7–8 is a common number and there may be as many as 12, as in *Polietes lardaria*, or even 18, as in *Mesembrina*.

IV. *The anal or perianal plate*

Frequent references have been made to this structure in the separate accounts of the different anthomyids.

As far as I can ascertain no previous observers have paid much attention to the variation and distribution of the anal plate, and no one seems to have appreciated its systematic value. The first important fact which emerges is that, while this structure is present in distinct and easily recognizable form in all the anthomyid larvae I have examined, it is absent from the larvae of Calliphorinae such as *Calliphora*, *Lucilia* and *Protophormia*. In the calliphorines it is represented by a swollen and usually heavily spined area on the ventral surface of the last abdominal segment, but it never forms a distinct plate and is never detachable. While the number of anthomyid genera examined is only a very small proportion of the whole, it is a fairly representative selection especially of the higher forms. If *Hylemyia* is regarded as at all typical of the lower Anthomyidae, it seems very probable that the anal plate will prove to be a feature common to all members of this family. Furthermore, the anal plate is persistent and usually more obvious in the puparium where it has become more heavily chitinized and more easily detached.

It is absent naturally from the puparia of Calliphorinae.

The second important fact which emerges is that the anal plate has a fairly uniform appearance in the different larvae examined, irrespective of whether they are saprophagous or carnivorous. That of *Morellia* departs a little from this standard type in having relatively slender lateral arms. That of *Musca domestica* (Figs. 140, 141), however, is of quite unique form and differs remarkably from all the others, in that the lateral arms are almost completely reduced so that the plate is short, squat and roughly butterfly-shaped. On this feature alone the larva of *Musca* can easily be distinguished from all the other dung-frequenting larvae I have examined. Since the anal plate is persistent in the puparium, it forms a very useful diagnostic character for *Musca* in that stage also.

I wish to thank Dr R. A. Staig of the Zoology Department of Glasgow University for his constant valuable advice and encouragement and for placing at my disposal the rich material of the King collection of Diptera.

I am greatly indebted to Prof. D. Keilin of Cambridge, not only for his kindness in directing my first scattered observations into systematic scientific channels, but also for supplying, through the medium of his numerous writings, a constant source of information and reference which has proved invaluable in facilitating the course of my investigations.

Key to lettering of Text-figures

an.s.	angular sclerites.	*m.d.s.*	median dorsal sclerite.
ant.	antennae.	*m.v.a.*	median ventral arch.
a.pl.	anal plate.	*mx.p.*	maxillary palps.
a.r.	anterior rods.	*o.b.*	oral bars.
a.sc.	accessory sclerites.	*or.gr.*	oral grooves.
a.sp.	anterior spiracles.	*p.a.l.*	post anal lobes.
B.	basal piece or pharyngeal sclerite.	*pal.h.*	palmate hairs.
C.	sensory organ C.	*par.s.*	parastomal sclerites.
co.p.	connecting pieces.	*ph.r.*	pharyngeal ridges.
d.b.	anterior dorsal bridge or arch.	*po.p.*	pointed pieces.
d.c.	dorsal cornua.	*po.r.*	posterior ribbon.
d.sc.	dental sclerite.	*ps.gl.*	perispiracular glands.
d.st.	dorsal strip.	*p.sp.*	posterior spiracles.
ex.s.	external scar.	*pu.sp.*	pupal spiracles or pupal horns.
in.p.s.	intrapupal spiracles.	*sb.t.*	suprabuccal teeth.
l.h.	lateral hooks or lateral crotchets.	*sl.d.*	salivary duct.
l.p.	labial palps.	*s.o.*	sensory organ.
l.sc.	labiate sclerite.	*to.sc.*	tongue-like sclerite.
M.	Middle piece, intermediate piece or hypostomal sclerite.	*t.sc.*	*t*-piece (labium).
		t.v.a.	transverse ventral arch.
m.	1st stage middle piece.	*v.c.*	ventral cornua.

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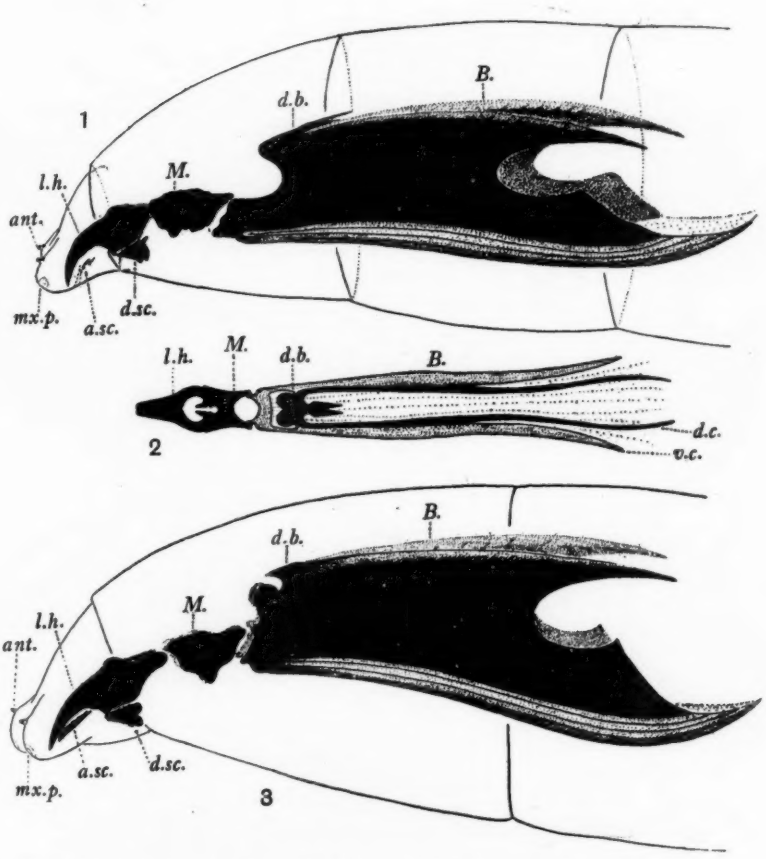


Fig. 1. *Cryptolucilia*. Anterior end of 3rd stage larva showing skeleton. ×77.
Fig. 2. *Cryptolucilia*. 3rd stage larva, dorsal view of buccopharyngeal armature. ×72.
Fig. 3. *Dasyphora*. 3rd stage larva, anterior end showing skeleton. ×74.

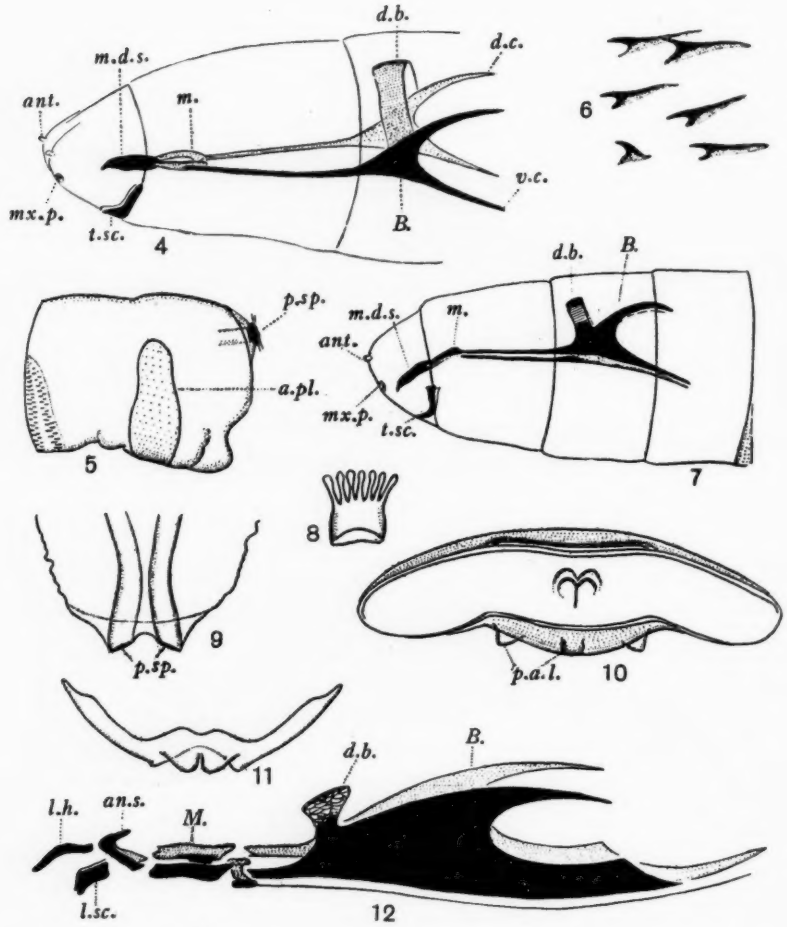


Fig. 4. *Cryptolucilia*. 1st stage larva, anterior end with skeleton. ×162.
Fig. 5. *Cryptolucilia*. 1st stage larva, posterior end. ×77.
Fig. 6. *Dasyphora*. Spines from ventral abdominal spine pad of 1st stage larva. ×875.
Fig. 7. *Dasyphora*. 1st stage larva, anterior end showing skeleton. ×95.
Fig. 8. *Dasyphora*. 3rd stage larva, anterior spiracles. ×78.
Fig. 9. *Dasyphora*. 1st stage larva. Dorsal view of posterior end showing posterior spiracles. ×85.
Fig. 10. *Dasyphora*. 3rd stage larva, anal plate, internal view. ×45.
Fig. 11. *Cryptolucilia*. 3rd stage larva, anal plate, posterior view. ×17.
Fig. 12. *Cryptolucilia*. 2nd stage larva, buccopharyngeal armature. ×105.

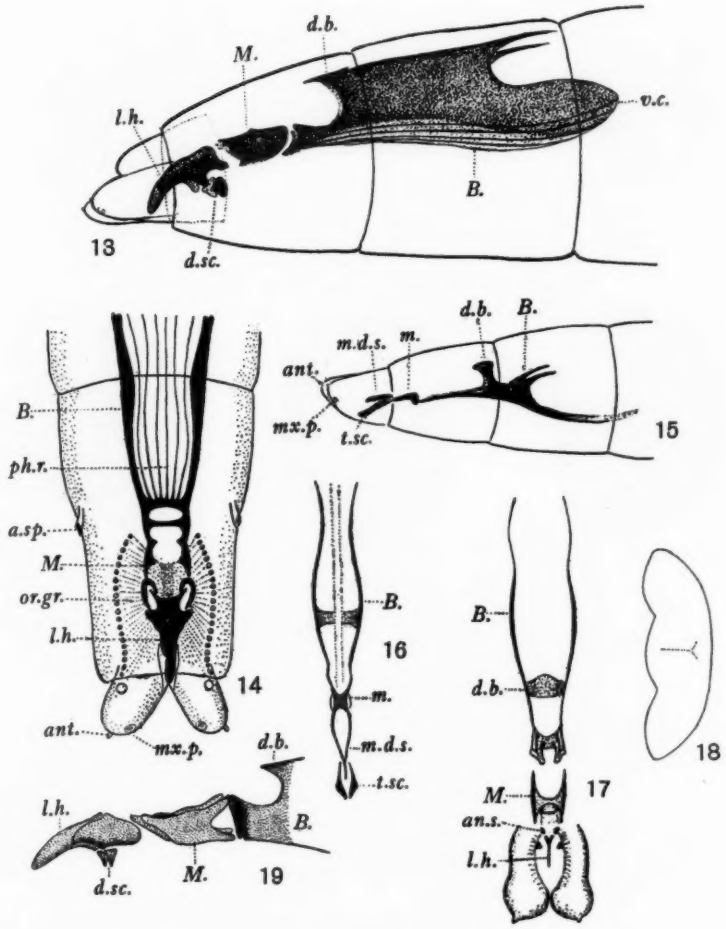
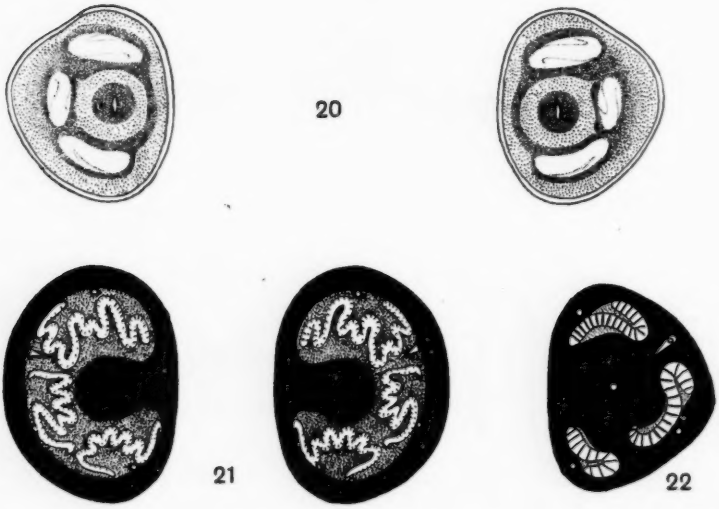


Fig. 13. *Haematobia*. 3rd stage larva, anterior end showing skeleton. ×75.
Fig. 14. *Haematobia*. 3rd stage larva, ventral view of mouth and associated structures. ×122.
Fig. 15. *Haematobia*. 1st stage larva, anterior end to show skeleton. ×77.
Fig. 16. *Haematobia*. 1st stage larva, ventral view of skeleton. ×111.
Fig. 17. *Haematobia*. 2nd stage larva, ventral view of skeleton. ×86.
Fig. 18. *Haematobia*. 3rd stage larva, anal plate. ×38.
Fig. 19. *Stomoxys*. 3rd stage larva, anterior part of skeleton. ×68.



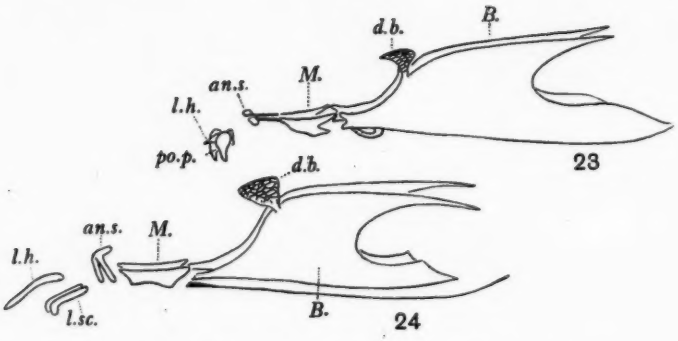


Fig. 20. *Haematobia*. 3rd stage larva, posterior spiracles. ×210.
Fig. 21. *Mesembrina*. 3rd stage larva, posterior spiracles. ×56.
Fig. 22. *Stomoxys*. 3rd stage larva, posterior spiracles. ×205.
Fig. 23. *Haematobia*. 2nd stage larva, skeleton. ×94.
Fig. 24. *Dasyphora*. 2nd stage larva, skeleton. ×97.

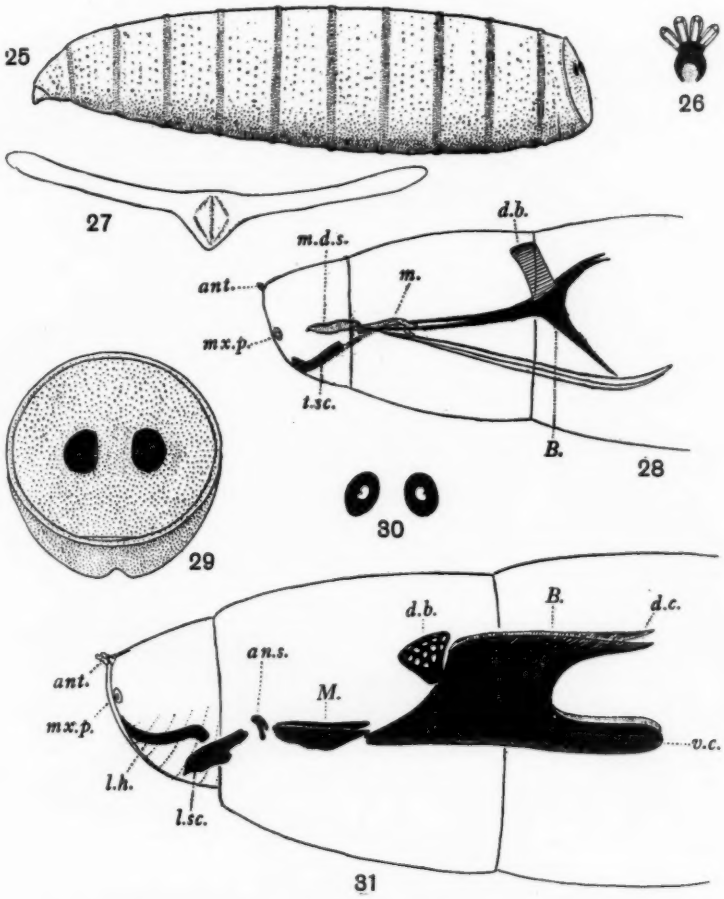


Fig. 25. *Morellia*. Mature 3rd stage larva. ×9.
Fig. 26. *Morellia*. 3rd stage larva, anterior spiracles. ×82.
Fig. 27. *Morellia*. 3rd stage larva, anal plate. ×38.
Fig. 28. *Morellia*. 1st stage larva, anterior end with skeleton. ×112.
Fig. 29. *Morellia*. 3rd stage larva, posterior end. ×13·8.
Fig. 30. *Morellia*. 1st stage larva, posterior spiracles. ×114.
Fig. 31. *Morellia*. 2nd stage larva, anterior end with skeleton. ×92.

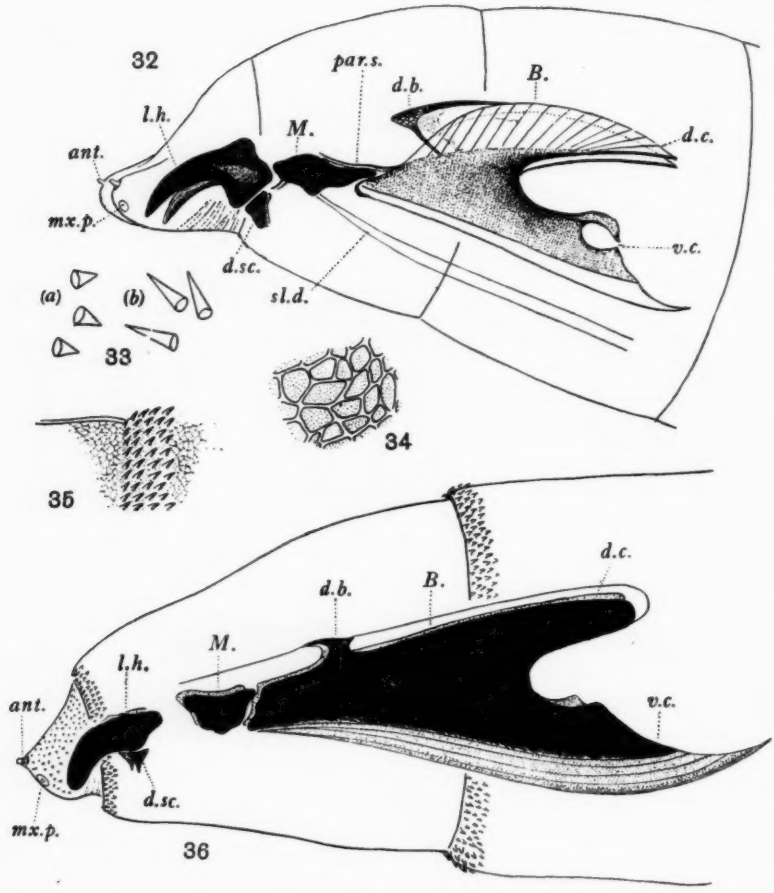


Fig. 32. *Hylemyia*. 3rd stage larva, anterior end with skeleton. ×82.
Fig. 33. *Morellia*. 3rd stage larva, spines from (*a*) middle of body, and (*b*) last segment of body. ×240.
Fig. 34. *Morellia*. 3rd stage larva, part of cuticle enlarged. ×102.
Fig. 35. *Morellia*. 3rd stage larva, spines on circumsegmental spine band. ×64.
Fig. 36. *Morellia*. 3rd stage larva, anterior end with skeleton. ×75.

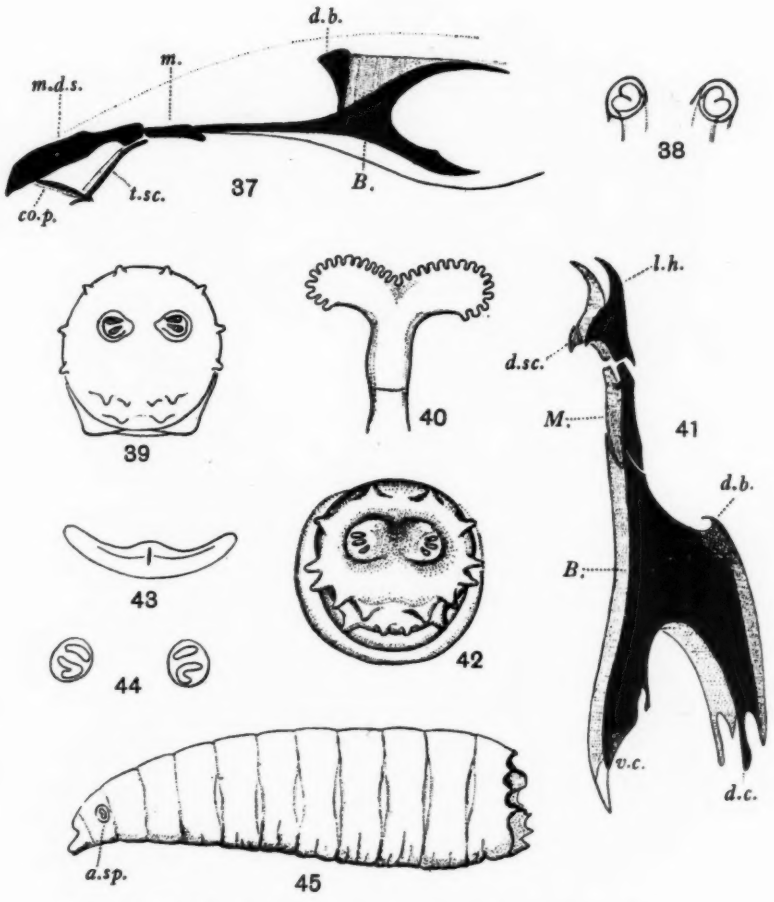


Fig. 37. *Hylemyia*. 1st stage larva, skeleton from exuvium. ×102.
Fig. 38. *Hylemyia*. 1st stage larva, posterior spiracles. ×78.
Fig. 39. *Hylemyia*. 2nd stage larva, posterior end. ×31.
Fig. 40. *Hylemyia*. 2nd or 3rd stage larva, anterior spiracles. ×105.
Fig. 41. *Hylemyia*. 2nd stage larva, skeleton from exuvia. ×68.
Fig. 42. *Hylemyia*. 3rd stage larva, posterior end. ×12.
Fig. 43. *Hylemyia*. 3rd stage larva, anal plate. ×24.
Fig. 44. *Morellia*. 2nd stage larva, posterior spiracles. ×72.
Fig. 45. *Hylemyia*. Mature 3rd stage larva. ×8·3.

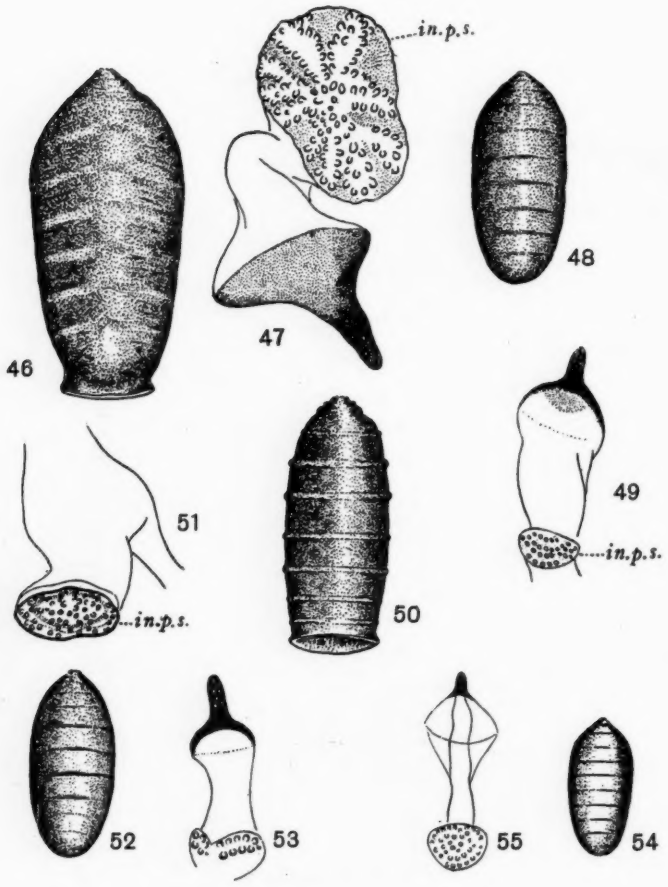


Fig. 46. *Mesembrina*. Puparium. ×4·5.
Fig. 47. *Mesembrina*. Prothoracic nymphal spiracles. ×77.
Fig. 48. *Dasyphora*. Puparium. ×4·5.
Fig. 49. *Dasyphora*. Prothoracic nymphal spiracles. ×71.
Fig. 50. *Morellia*. Puparium. ×4·5.
Fig. 51. *Morellia*. Prothoracic nymphal spiracles. ×54.
Fig. 52. *Cryptolucilia*. Puparium. ×4·5.
Fig. 53. *Cryptolucilia*. Prothoracic nymphal spiracles. ×82.
Fig. 54. *Haematobia*. Puparium. ×4·5.
Fig. 55. *Haematobia*. Prothoracic nymphal spiracles. ×80.

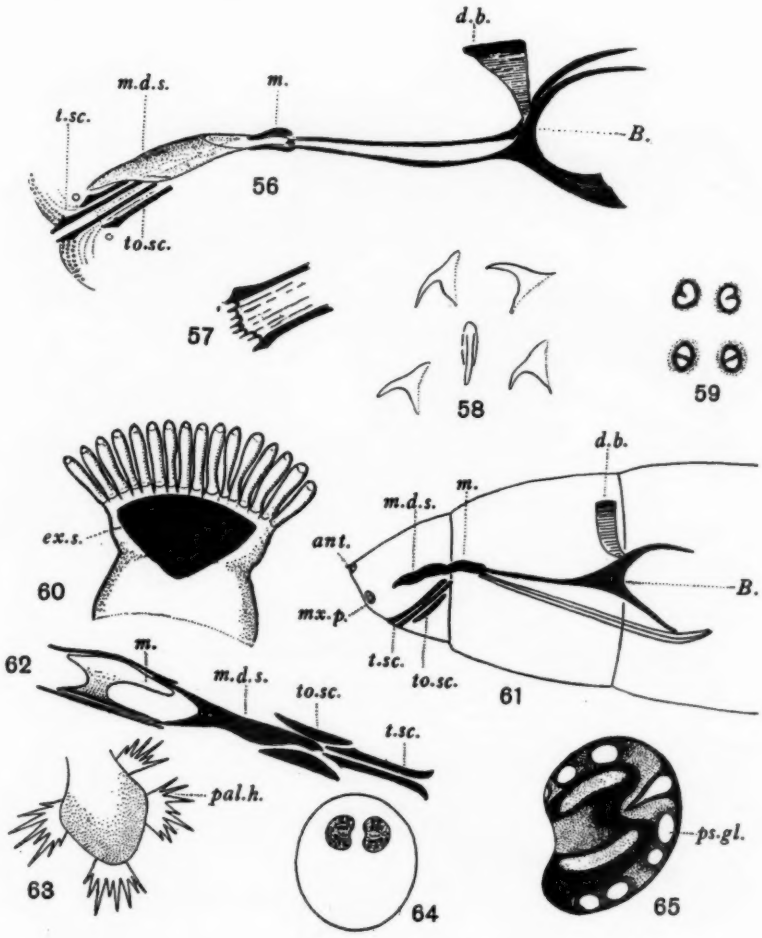


Fig. 56. *Mesembrina*. 1st stage larva, skeleton from exuvium. ×100.
Fig. 57. *Mesembrina*. 1st stage larva, tongue-like sclerite. ×123.
Fig. 58. *Mesembrina*. Ventral spines from 1st stage larva. ×818.
Fig. 59. *Mesembrina*. 1st stage larva, posterior spiracles. ×119.
Fig. 60. *Mesembrina*. 3rd stage larva, anterior spiracles. ×95.
Fig. 61. *Polietes hirticrura*. 1st stage larva, anterior end to show skeleton. ×140.
Fig. 62. *Polietes*. Buccal sclerites from 1st stage exuvium. ×295.
Fig. 63. *Polietes*. 1st stage larva, posterior spiracles from exuvium. ×272.
Fig. 64. *Polietes*. 2nd stage larva, posterior end showing spiracles. ×47.
Fig. 65. *Polietes*. 2nd stage larva, posterior spiracles. ×199.

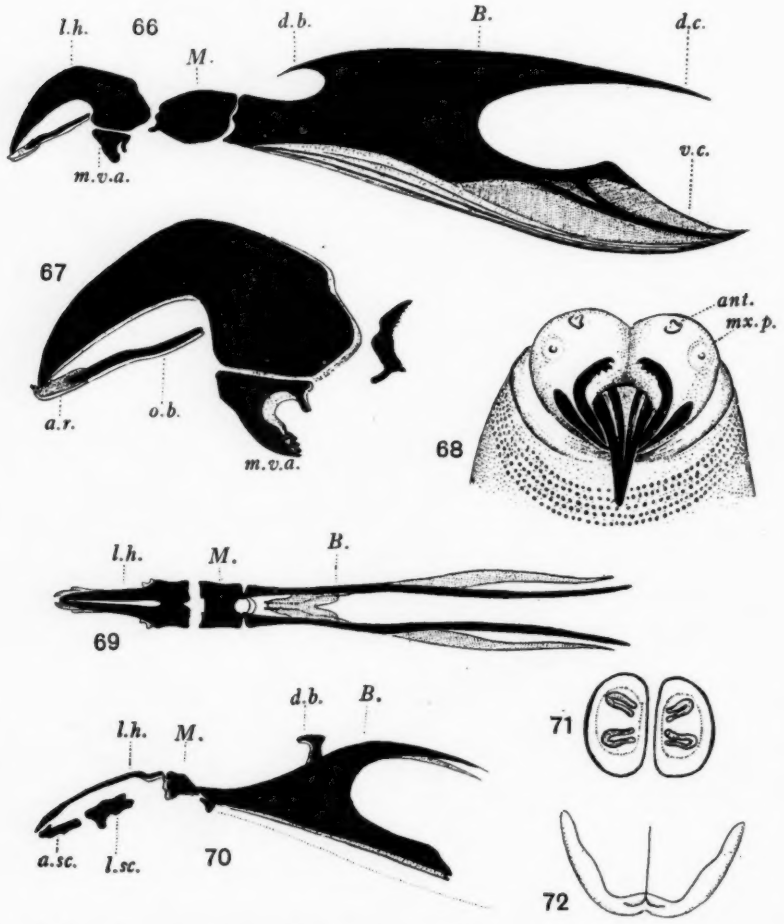


Fig. 66. *Mesembrina*. 3rd stage larva, skeleton. ×42.
Fig. 67. *Mesembrina*. Anterior part of skeleton more enlarged. ×99.
Fig. 68. *Mesembrina*. Mature 3rd stage larva, head with mouth-parts extended. ×19.
Fig. 69. *Mesembrina*. 3rd stage larva, dorsal view of skeleton. ×35.
Fig. 70. *Mesembrina*. 2nd stage larva, skeleton. ×61.
Fig. 71. *Mesembrina*. 2nd stage larva, posterior spiracles. ×59.
Fig. 72. *Mesembrina*. Anal plate of 3rd stage larva. ×6.

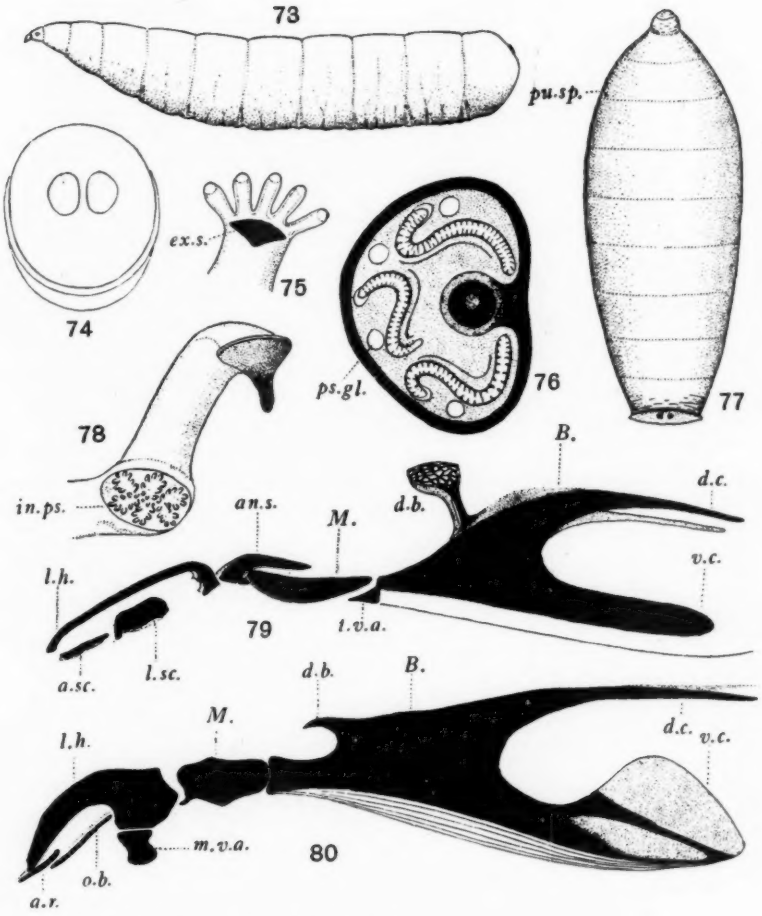


Fig. 73. *Polietes*. 3rd stage mature larva. ×5·3.
Fig. 74. *Polietes*. 3rd stage larva, posterior end showing relations of spiracular plates. ×34.
Fig. 75. *Polietes*. 3rd stage larva, anterior spiracles. ×243.
Fig. 76. *Polietes*. 3rd stage larva, posterior spiracles. ×176.
Fig. 77. *Polietes*. Puparium. ×7·5.
Fig. 78. *Polietes*. Prothoracic nymphal spiracles. ×78.
Fig. 79. *Polietes*. 2nd stage larva, skeleton. ×191.
Fig. 80. *Polietes*. 3rd stage larva, skeleton. ×86.

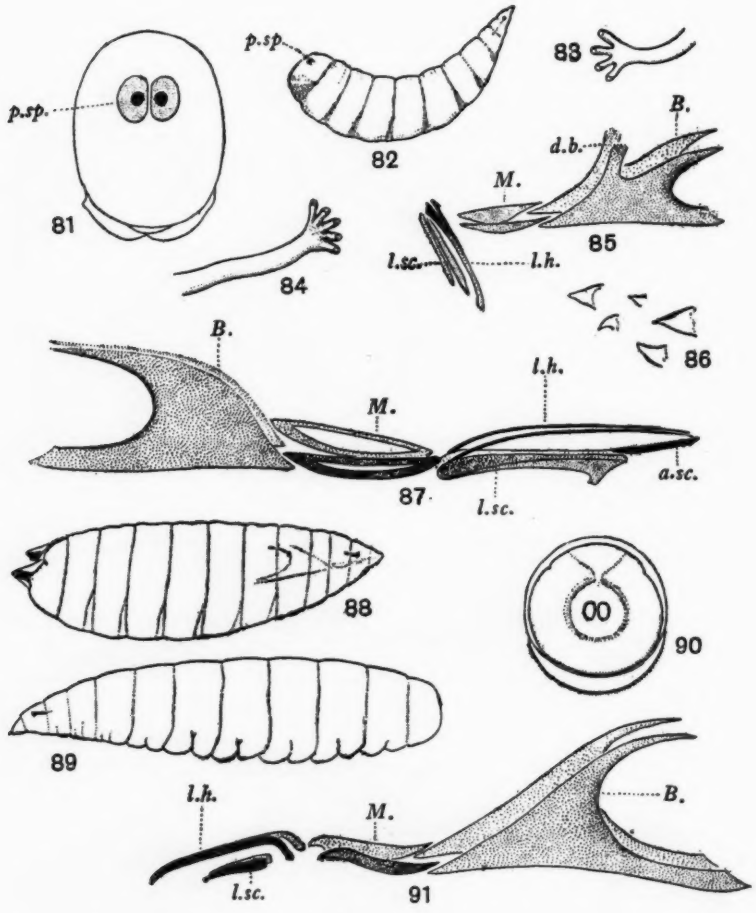


Fig. 81. *Myiospila*. 2nd stage larva, posterior end. ×68.
Fig. 82. *Mydaea urbana*. Newly hatched. 2nd stage larva. ×23.
Fig. 83. *Myiospila*. 2nd stage larva, anterior spiracles. ×341.
Fig. 84. *Mydaea urbana*. 2nd stage larva, anterior spiracles. ×273.
Fig. 85. *Myiospila*. 2nd stage larva, skeleton. ×152.
Fig. 86. *Mydaea urbana*. 2nd stage larva, ventral spines. ×545.
Fig. 87. *Mydaea urbana*. 2nd stage larva, skeleton. ×191.
Fig. 88. *Hebecnema*. Newly hatched, 2nd stage larva. ×54.
Fig. 89. *Hebecnema*. Mature 3rd stage larva. ×11·3.
Fig. 90. *Hebecnema*. Mature 3rd stage larva, posterior end. ×29.
Fig. 91. *Hebecnema*. 2nd stage larva, skeleton. ×346.

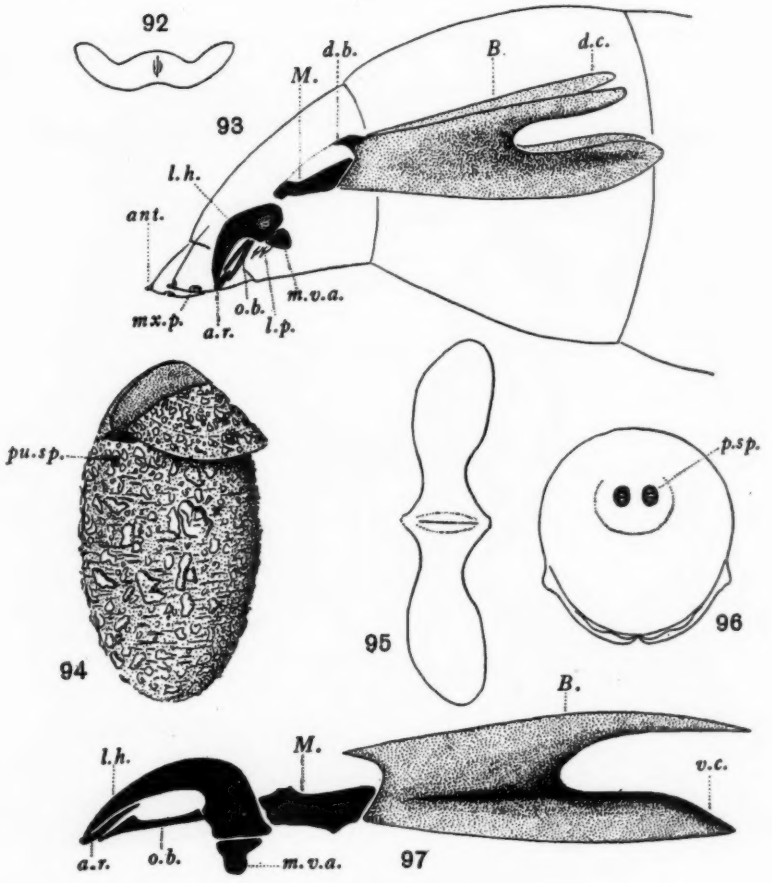


Fig. 92. *Hebecnema*. Anal plate of 3rd stage larva. ×44.

Fig. 93. *Hebecnema*. 3rd stage larva, anterior end to show skeleton. ×136.

Fig. 94. *Mydaea urbana*. Puparium. ×8·3.

Fig. 95. *Mydaea urbana*. Anal plate of 3rd stage larva. ×48.

Fig. 96. *Mydaea urbana*. Posterior end of mature 3rd stage larva, showing relation of spiracles. ×14.

Fig. 97. *Mydaea urbana*. Early 3rd stage larva, skeleton. ×98.

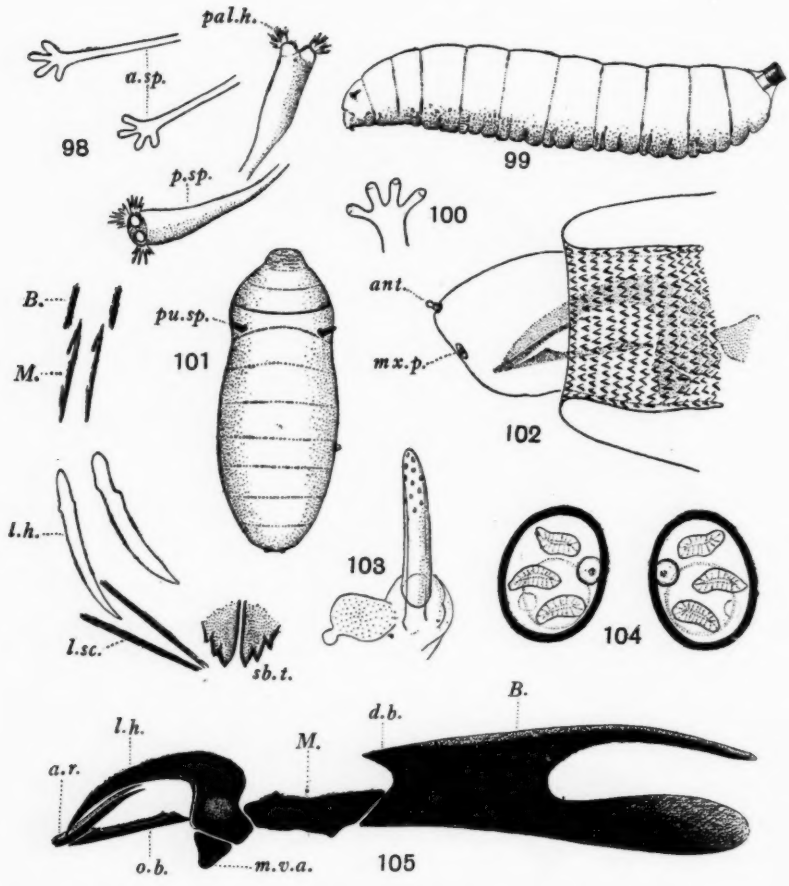
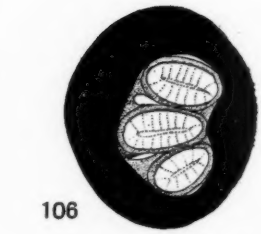


Fig. 98. *Mydaea pagana*. Exuvium of 2nd stage larva extracted from egg. ×137.
Fig. 99. *Mydaea pagana*. Newly hatched 3rd stage larva. ×21.
Fig. 100. *Mydaea pagana*. Anterior spiracles of 3rd stage larva. ×263.
Fig. 101. *Hebecnema*. Puparium. ×11·3.
Fig. 102. *Mydaea pagana*. Anterior end of 3rd stage larva, showing infolding of spine band. ×180.
Fig. 103. *Hebecnema*. Prothoracic nymphal spiracles. ×100.
Fig. 104. *Mydaea pagana*. Posterior spiracles of newly hatched 3rd stage larva. ×188.
Fig. 105. *Mydaea pagana*. 3rd stage larva, skeleton. ×142.



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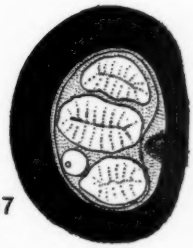

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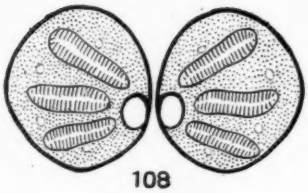

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Fig. 106. *Myiospila*. Late 3rd stage larva, posterior spiracles. ×221.
Fig. 107. *Mydaea urbana*. Late 3rd stage larva, posterior spiracles. ×175.
Fig. 108. *Myiospila*. Early 3rd stage larva, posterior spiracles. ×235.
Fig. 109. *Muscina*. Early 3rd stage larva, posterior spiracles. ×128.
Fig. 110. *Muscina*. Late 3rd stage larva, posterior spiracles. ×104.

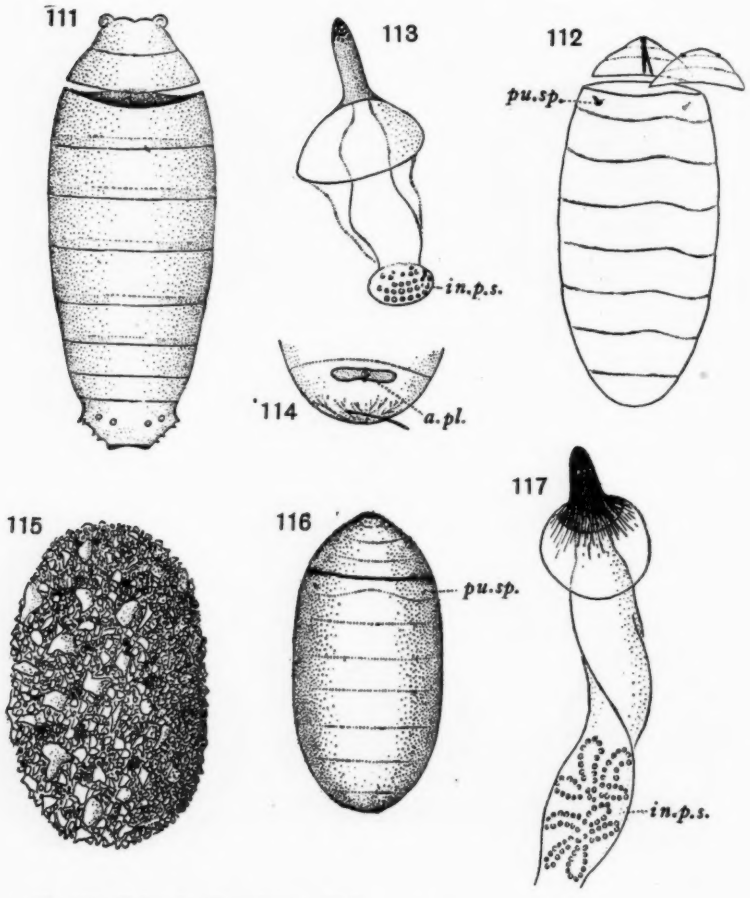


Fig. 111. *Hylemyia*. Puparium. ×14·3.
Fig. 112. *Phaonia*. Puparium after eclosion. ×7·5.
Fig. 113. *Phaonia*. Prothoracic nymphal spiracles. ×56.
Fig. 114. *Phaonia*. Posterior end of puparium to show ventral anal plate. ×11·3.
Fig. 115. *Muscina*. Earthen cocoon. ×5·3.
Fig. 116. *Muscina*. Puparium extracted from cocoon. ×5·3.
Fig. 117. *Muscina*. Prothoracic nymphal spiracles. ×88.

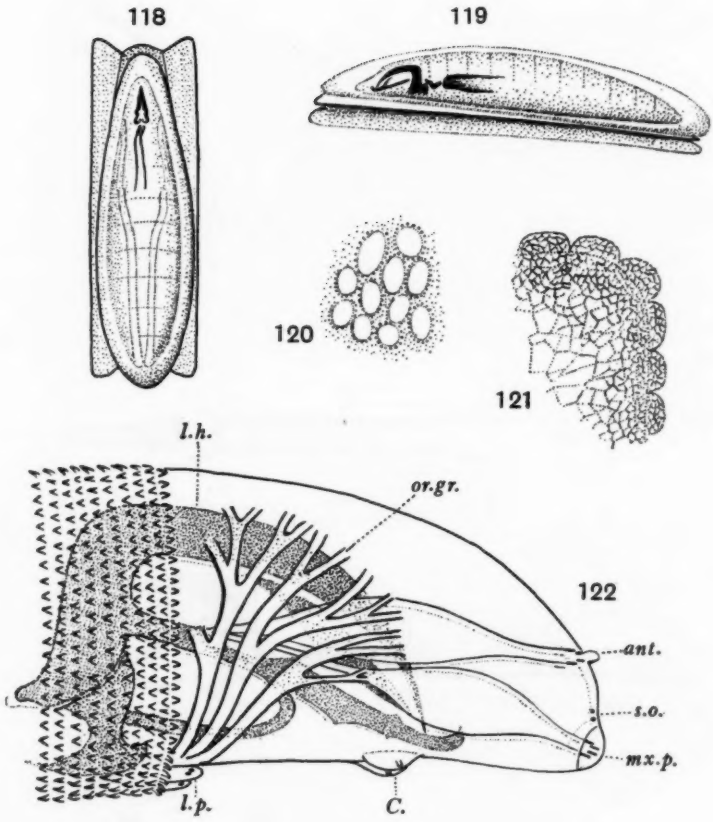


Fig. 118. *Phaonia*. Dorsal view of egg cleared just prior to hatching. ×31.
Fig. 119. *Phaonia*. Lateral view of egg before hatching. ×38.
Fig. 120. *Phaonia*. Part of sculptured chorion of egg. ×261.
Fig. 121. *Phaonia*. Edge of flange of egg showing marginal lobes. ×239.
Fig. 122. *Phaonia*. Head of newly hatched 3rd stage larva. ×386.

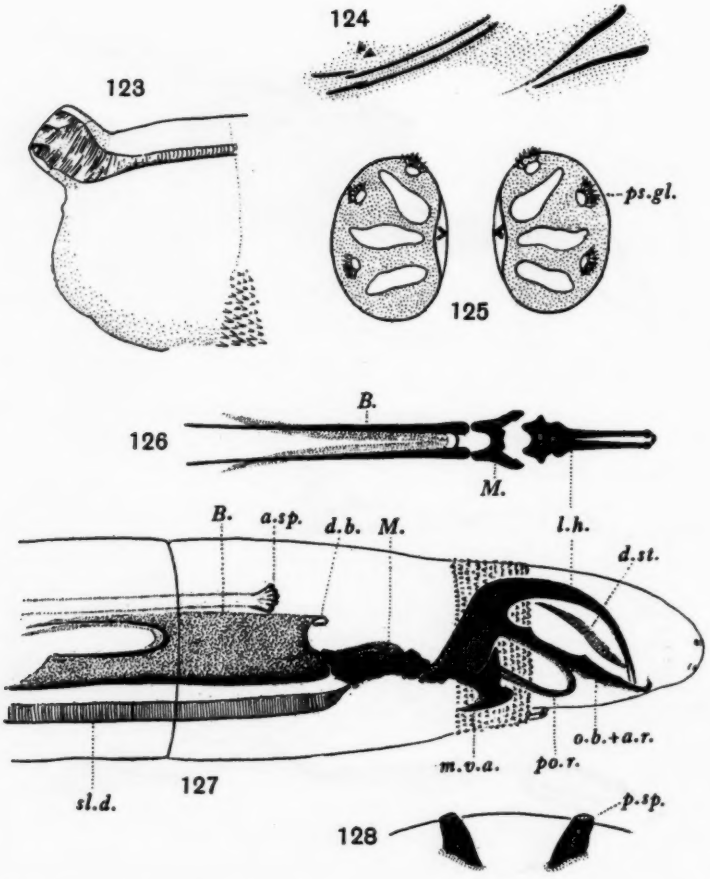


Fig. 123. *Phaonia*. Newly hatched 3rd stage larva, posterior end showing spiracles. ×142.
Fig. 124. *Phaonia*. Exuvium of early stage larva, extracted from egg. ×252.
Fig. 125. *Phaonia*. Newly hatched 3rd stage larva, posterior spiracles. ×230.
Fig. 126. *Phaonia*. Dorsal view of early 3rd stage skeleton. ×98.
Fig. 127. *Phaonia*. Newly hatched 3rd stage larva, anterior end showing skeleton. ×128.
Fig. 128. *Phaonia*. Posterior spiracles of late 3rd stage larva. ×62.

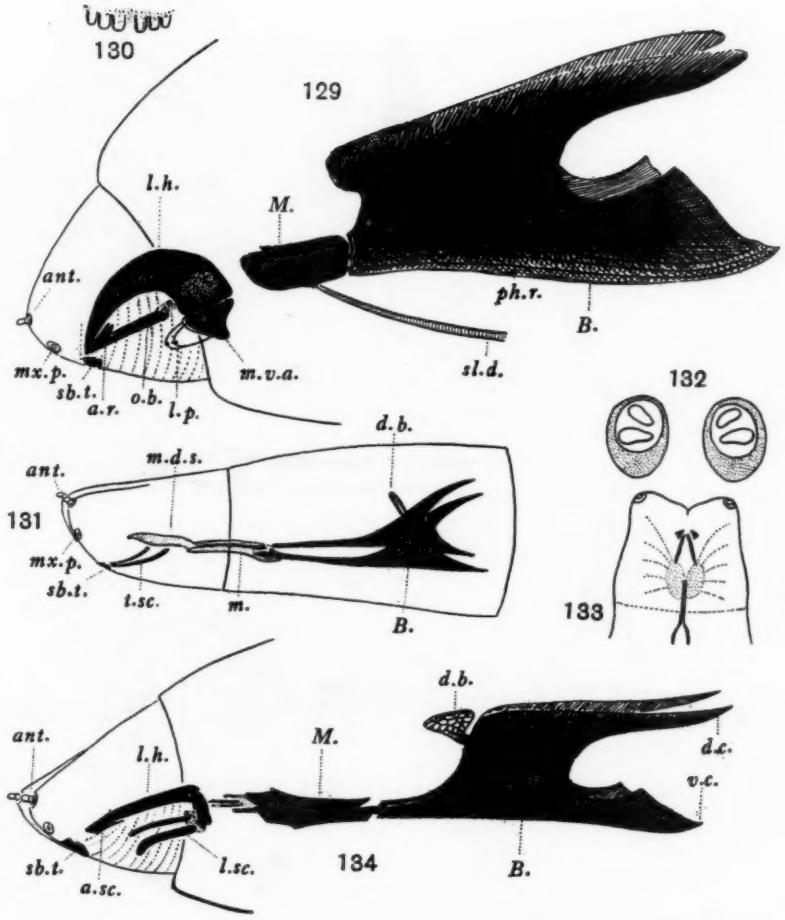


Fig. 129. *Muscina*. Mature 3rd stage larva, anterior end with skeleton. ×75.
Fig. 130. *Muscina*. Suprabuccal teeth of 3rd stage larva. ×187.
Fig. 131. *Muscina*. 1st stage larva, anterior end with skeleton. ×204.
Fig. 132. *Muscina*. 2nd stage larva, posterior spiracles. ×188.
Fig. 133. *Muscina*. 1st stage larva, ventral view of head. ×166.
Fig. 134. *Muscina*. 2nd stage larva, anterior end with skeleton. ×177.

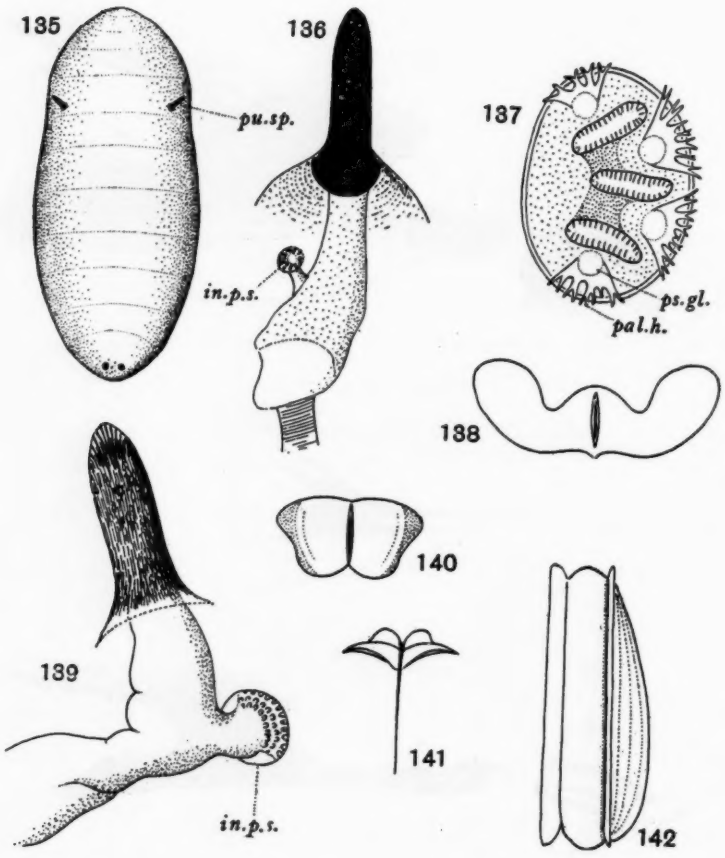
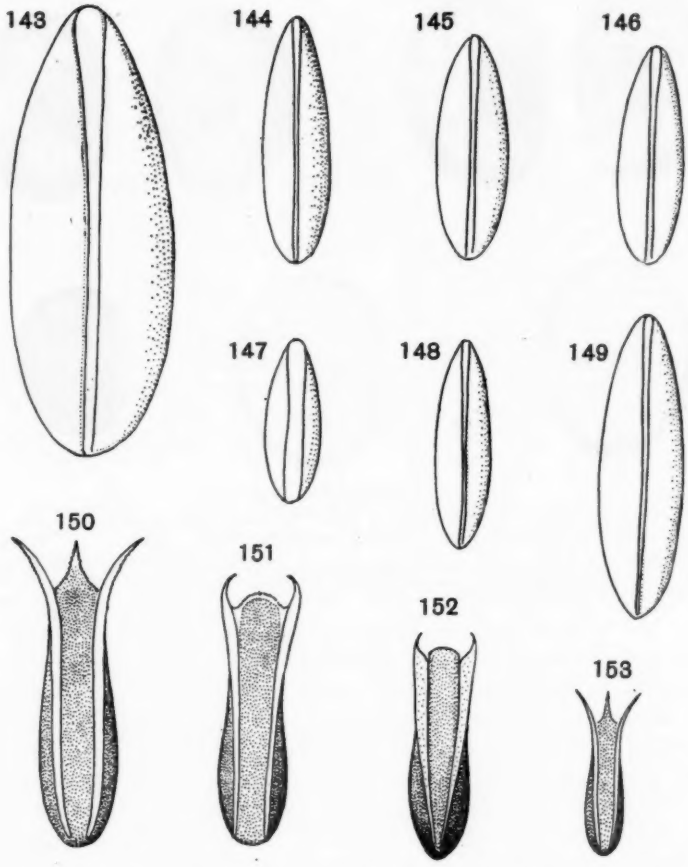


Fig. 135. *Mydaea pagana*. Puparium. ×9.
Fig. 136. *Mydaea pagana*. Prothoracic nymphal spiracles. ×90.
Fig. 137. *Hebecnema*. Posterior spiracles of mature 3rd stage larva. ×409.
Fig. 138. *Mydaea pagana*. Anal plate from puparium. ×40.
Fig. 139. *Mydaea urbana*. Prothoracic nymphal spiracles. ×100.
Fig. 140. *Musca domestica*. Anal plate of 3rd stage larva and puparium, ventral view. ×74.
Fig. 141. *Musca domestica*. Anal plate, posterior view. ×56.
Fig. 142. *Muscina*. Egg. ×29.



Figs. 143–153. Eggs of dung-frequenting anthomyids drawn to scale, all × 15.

Fig. 143. *Mesembrina.*
Fig. 144. *Dasyphora.*
Fig. 145. *Cryptolucilia.*
Fig. 146. *Morellia.*
Fig. 147. *Haematobia.*
Fig. 148. *Polietes hirticrura.*
Fig. 149. *Polietes lardaria.*
Fig. 150. *Mydaea urbana.*
Fig. 151. *Mydaea pagana.*
Fig. 152. *Myiospila.*
Fig. 153. *Hebecnema.*

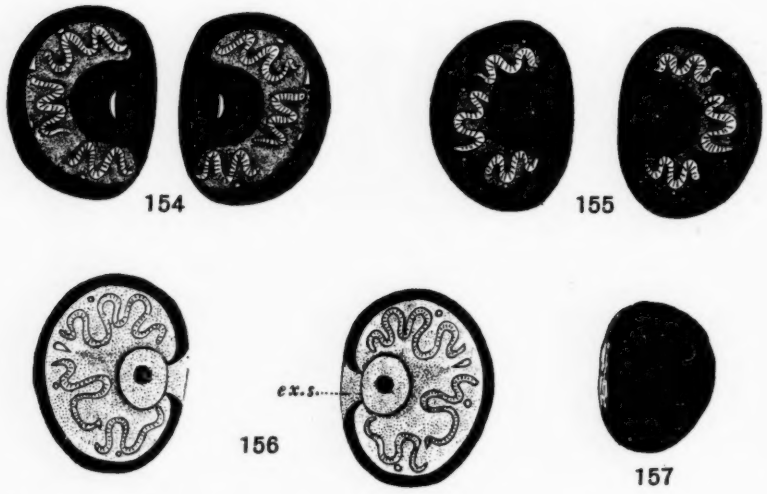


Fig. 154. *Cryptolucilia*. Posterior spiracles of mature 3rd stage larva. ×89.
Fig. 155. *Dasyphora*. Posterior spiracles of mature 3rd stage larva. ×106.
Fig. 156. *Morellia*. Posterior spiracles of 3rd stage larva, treated to show the spiracular slits. ×91.
Fig. 157. *Morellia*. Posterior spiracles of late 3rd stage larva. ×68.

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THE TREMATODE PARASITES FROM A RED-BELLIED WATERSNAKE, *FARANCIA ABACURA*

By ELON E. BYRD
Zoology Department, University of Georgia

(With 5 Figures in the Text)

A NUMBER of trematode parasites were taken from the digestive tract of a red-bellied watersnake, *Farancia abacura* (Holbrook), on 27 March 1933. This snake had been captured on the previous day from a canal at Harvey, Louisiana. The parasites were studied while still alive and were tentatively identified before being fixed with formalin while under the pressure of a cover-slip. Representatives of three genera were encountered. Two of the species, representing two separate genera, are considered by us to be new to science and are herein described under the proposed names of *Cercorchis auridistomi* n.sp. and *Stomatrema guberleti* n.sp. The third species was recognized as *Vitellotrema fusipora* Guberlet, 1928.

Cercorchis auridistomi n.sp.

(Figs. 1 and 2)

Description: Cercorchis. Body elongated, slightly flattened ventrally, with bluntly rounded ends and parallel sides, averaging 2·26 mm. long by 0·52 mm. wide. Cuticula beset with fine spines anteriorly to about level of ovary. Oral sucker subterminal, 0·15 mm. long by 0·21 mm. wide, possessing two antero-lateral lip-like appendages which extend beyond outer boundary of sucker for a distance of about 26μ on either side (these structures seen to originate from the region of the oral opening as though they were lateral lips). Acetabulum 0·14 mm. long by 0·17 mm. wide, lying approximately 0·45 mm. from anterior margin of body. Prepharynx present, short. Pharynx 0·07 mm. long by 0·11 mm. wide, surrounded by numerous rather large peripharyngeal gland cells. Oesophagus short, about 87μ long, bearing relatively few peri-oesophageal gland cells. Caeca uniform, almost straight, ending at caudal boundary of posterior testis. Ovary transversely oval, 0·10 mm. long by 0·22 mm. wide, placed slightly to right of midline, lying 0·170 mm. behind caudal margin of acetabulum. Laurer's canal and receptaculum seminis unobserved. Shell gland present. Uterus distinct, descending and ascending limbs slightly overlapping in midline, and overlapping caeca; descending on right side of body by a series of wavy loops to level of anterior testis, ascending on opposite side of body by similar loops to genital pore (in second specimen the descending and ascending limbs cross to opposite sides of body at a level approximating two-thirds the distance from ovary to anterior testis); uterus making one rather long loop and

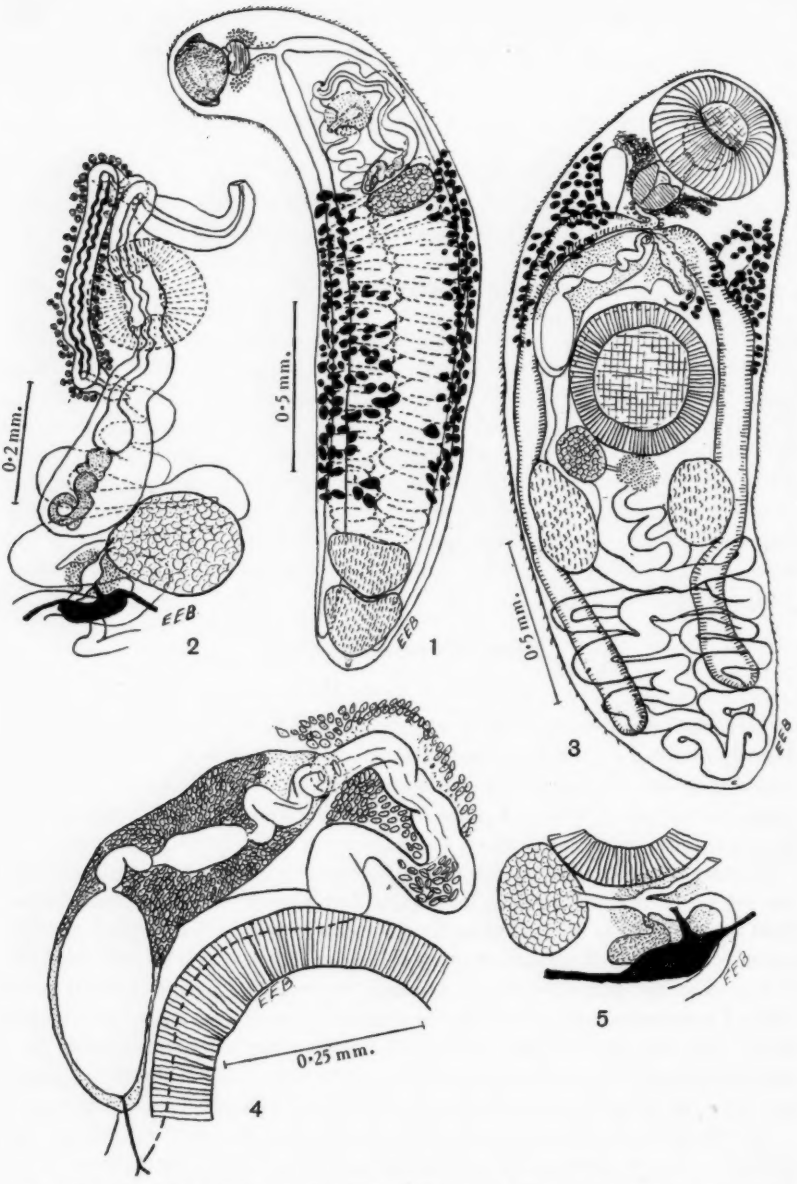

Fig. 1. *Cercorchis auridistomi* n.sp. Details of the internal organization. Dorsal view. ×24. (All figures drawn by the aid of the camera lucida unless otherwise stated.)
Fig. 2. *Cercorchis auridistomi* n.sp. Details of the metraterm, cirrus sac, and ovarian complex. Dorsal view. ×60.
Fig. 3. *Stomatrema guberleti* n.sp. Details of the internal organization. Ventral view. ×24.
Fig. 4. *Stomatrema guberleti* n.sp. Details of the cirrus sac, genital pore, and metraterm. Ventral view. ×60.
Fig. 5. *Stomatrema guberleti* n.sp. Details of the ovarian complex. Ventral view. Diagrammatic.

two or three short loops in front of ovary before forming metraterm. Metraterm well developed, carrying many rather large and conspicuous perivaginal gland cells, extending about two-thirds length of cirrus sac. Ova numerous, operculated, from 15 to 18μ by 30 to 36μ in dimensions. Vitellaria follicular, mainly lateral to caeca but spreading far enough to overlap caeca and outer limits of uterus, extending from level of ovary to near anterior margin of anterior testis (in second specimen the vitelline glands on the left side extend posteriorly to about the equatorial plane of the anterior testis). Yolk ducts single on each side, uniting in region of oötype where they form small yolk reservoir. Testes in tandem at posterior extremity of body; anterior testis, 0·165 mm. long by 0·260 mm. wide, rounded posteriorly, flattened anteriorly; posterior testis, 0·170 mm. long by 0·220 mm. wide, rounded posteriorly, slightly concave anteriorly, placed close behind anterior testis. Vasa efferentia arising from medio-dorsal portion of anterior margins of testes, uniting a short way before entering cirrus sac. Cirrus sac long, slightly club-shaped, convoluted, extending from genital pore around left side of acetabulum to ovary, containing small sacculate, slightly coiled vesicula seminalis, a bulbous pars prostatica with numerous gland cells, a long ductus, and well-developed cirrus (in one specimen the cirrus is exserted, in which condition it measures 0·212 mm. in length). Genital pore ventral, slightly to left of midline, about 60μ in front of acetabulum. Excretory bladder median, long, giving rise to cornua at about level of ovary; cornua ending posterior to level of acetabulum. Flame cell formula undetermined.

Host: Farancia abacura (Holbrook).

Habitat: Upper small intestine.

Locality: North America (United States, Harvey, Louisiana).

Type specimen: Writer's private collection, Zoology Department, University of Georgia, U.S.A.

Cercorchis auridistomi is at variance with the characters of the genus to which it is assigned in respect of the lip-like appendages that arise from the region of the oral opening and spread laterally far enough to become exposed beyond the outer boundaries of the sucker, and in respect of the vitellaria. In regard to the last named character the form appears to be more like a member of the genus *Protens*. The position of the genital pore, the position of the ventral sucker, ovary and testes, the arrangement of the uterus, and the type of excretory bladder clearly distinguish the form as a member of the genus *Cercorchis*. The oral sucker with its lip-like appendages, and the distribution of the vitellaria, as well as the type of metraterm and the extensive overlapping of the caeca by the uterus distinguish the species as being unique within the genus *Cercorchis*.

Cercorchis auridistomi is represented in the writer's collection by one complete specimen and two fragments. Two entire worms and the posterior half of another were recovered from the host. In remounting one of the worms the anterior end from about the level of the bifurcation of the caeca became

detached and was lost. The posterior portion of this worm is in excellent condition for studying the anatomy of that portion of the body; in some respects it is superior to the entire specimen.

Stomatrema guberleti n.sp.

(Figs. 3, 4 and 5)

Description: Stomatrema. Body elongated oval in outline, slightly flattened ventrally, strongly arched dorsally, measuring 2·24 mm. long by 0·82 mm. wide; widest just in front of acetabulum. Cuticula relatively thin, thickly beset with fine spines anteriorly; spines gradually diminishing toward posterior end where they finally disappear just before reaching posterior extremity. Oral sucker subterminal, wider than long, 0·36 mm. long by 0·40 mm. wide. Acetabulum larger, almost spherical, 0·48 mm. long by 0·46 mm. wide, lying just anterior to equator of body, or 0·78 mm. behind anterior margin of body. Prepharynx present, about 87μ long. Pharynx globular, 0·13 mm. in diameter, surrounded by numerous rather large and conspicuous peripharyngeal gland cells. Oesophagus about 0·10 mm. long, with few peri-oesophageal gland cells. Caeca more or less uniform, rather large, extending to within 0·27 mm. of posterior margin of body, overlapped by the uterus. Ovary oval, 0·175 mm. long by 0·14 mm. wide, with long axis diagonal to long axis of body, placed slightly right of midline at margin of right posterior quadrant of acetabulum. Laurer's canal, a relatively large, sac-shaped receptaculum seminis and shell gland present. Uterus greatly convoluted; descending limb making one complete transverse loop across body just posterior to testes, then descending by a series of short loops and coils ventral to left caecum to posterior extremity of body; ascending limb ascending by a similar series of loops and coils on opposite side of body to region just posterior to testes where it makes one complete transverse loop across body before swinging around right side of acetabulum to genital pore; uterus overlapping caeca posterior to level of testes. Metraterm well developed, about two-thirds length of cirrus sac, surrounded by conspicuous perivaginal gland cells. Ova numerous, operculated, measuring 15–17μ by 27–30μ. Vitellaria follicular, lateral in position, extending from level of posterior margin of oral sucker to level approximating equatorial plane of acetabulum, overlapping caeca. Yolk ducts single on each side, uniting in region of oötype to form small yolk reservoir. Testes opposite, in intercaecal space, closely opposed to caeca; right testis 0·36 mm. long by 0·14 mm. wide, placed so that its anterior margin lies on same level with equatorial plane of ovary; left testis 0·25 mm. long by 0·21 mm. wide, placed so that its posterior margin is on same level as posterior margin of right testis. Vasa efferentia uniting a short way before entering cirrus sac. Cirrus sac large, sausage-shaped, 0·59 mm. long by 0·15 mm. wide, extending from genital pore to level of equatorial plane of acetabulum, containing large vesicula seminalis that shows an anterior constriction, a large, muscular pars prostatica with

numerous rather well-defined prostatic gland cells, a short ductus, and a well-developed cirrus. Genital pore ventral, median, just behind bifurcation of caeca, forming a short genital sinus. Excretory pore slightly dorsal to termination of body, guarded by well-developed sphincter muscle; bladder median, long, Y-shaped, giving rise to cornua in region of ovary; cornua terminating just short of level of posterior margin of oral sucker. Flame cell formula undetermined.

Host: Farancia abacura (Holbrook).

Habitat: Oesophagus.

Locality: North America (United States, Harvey, Louisiana).

Type specimen: Writer's private collection, Zoology Department, University of Georgia, U.S.A.

Stomatrema guberleti is separated from its nearest relative, *S. pusilla* Guberlet, 1928, the only other species belonging to the genus, by its greater width, the larger suckers, the more cephalic position of the acetabulum, the more caudal position of the genital pore, the larger testes and ovary, the more caudal position of the vitellaria, and the type and extent of the uterus.

Vitellotrema fusipora Guberlet, 1928

Among the parasites removed from the oesophagus of the red-bellied watersnake a single adult specimen identified as *Vitellotrema fusipora* Guberlet, 1928, was recovered. Although the specimen shows a somewhat smaller body and smaller internal organs, as well as longer polar filaments to the slightly smaller eggs, it is believed to be identical with the species to which the specimen is assigned.

DISCUSSION

The trematode parasites removed from the alimentary canal of the red-bellied watersnake, *Farancia abacura*, and recorded in this paper belong to widely separated families. The species *Cercorchis auridistomi* and *Stomatrema guberleti* belong to the family PLAGIORCHIDAE Lühe, 1901 (= LEPODERMATIDAE Odhner, 1910), while *Vitellotrema fusipora* belongs to the family HALIPEGIDAE Poche, 1925. In regard to the last named species Guberlet (1928) is justified in the creation of the genus *Vitellotrema* for the reception of the form, *V. fusipora*, from the red-bellied watersnake, and in placing it in the family HALIPEGIDAE. Although our observations on the species are limited to a single adult specimen, it agrees with the specimens described by Guberlet in respect to the internal organs and in the size and shape of the vitelline glands, which, in our specimen, are paired glands, spherical or oval in outline and lie close behind and slightly lateral to the position of the ovary. The eggs in the present specimen are slightly smaller than the measurements given by Guberlet, and possess a polar filament slightly longer than the greatest length indicated in the original description. These variations, together with the variations indicated above, seem insufficient

for the creation of a new species for the form, nor do they warrant materially altering the original description of the species.

The systematic positions of the genera and subfamilies included in the family PLAGIORCHIDAE have been the subject of much discussion by recent workers. The writer prefers to reserve any discussion of the family group until some future date but is inclined to agree with Talbot (1934) in excluding the genus *Stomatrema* Guberlet from the subfamily RENIFERINAE Pratt (1902), and with Perkins (1928), Mehra (1931), and McMullen (1935) in placing the subfamily TELORCHIINAE in the family PLAGIORCHIDAE. The genus *Cercorchis* Lühe (1901) unquestionably belongs to the subfamily TELORCHIINAE as outlined by Perkins (1928). The question of subfamily relationship for the genus *Stomatrema* is more difficult, and can only be definitely settled after its life cycle has been worked out. It is most probable that the form will be found to show closer relations to the subfamilies LEPODERMATINAE Looss (1899) or STYPHLOTREMINAE Baer (1924) than to any other of the subfamilies of the family PLAGIORCHIDAE.

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A NEW SPECIES OF ACANTHOCEPHALA, *NEOECHINORHYNCHUS TOPSEYI* N.SP., FROM A CALCUTTA FISH, *POLYNEMUS HEPTADACTYLUS* (CUV. & VAL.)

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(With 3 Figures in the Text)

During the course of my investigation of the parasitic infection of various fishes of the Calcutta markets, I came across a new acanthocephalan parasite, *Neoechinorhynchus topseyi*, from the intestine of *Polynemus heptadactylus*, commonly known in Bengal as *Topsey* or mango-fish. The host was available in the local market during the months of February–August, and infection with this parasite marked during May–July. A single case was, however, noticed in August 1935 when after the intestine was taken out a portion of the thread-like parasite was seen hanging from its anal region. The intestine was slit open and it was found that one gravid female measuring $69 \times 1{\cdot}5$ mm. was the only occupant of the entire lumen of the gut. The parasite was attached by means of its proboscis to the anterior part of the intestine near the duodenum.

The body is long and cylindrical with a globular proboscis at the anterior end. The males are generally smaller than the females. The colour of the worms is creamy and sometimes whitish in freshly fixed specimens.

The proboscis is globular in shape with a very short neck. It is covered with three rows of six hooks each. Hooks of the anterior row are much longer than the other two rows. The proboscis sheath is a thin, single-layered, muscular sac (Fig. 1).

The body is devoid of spines. Its wall is traversed by a system of canals, the lacunar canals, which form a distinct network called the lacunar system (Verma & Datta, 1929). The body wall is composed of a thick outermost layer of cuticle, below which there is a thick layer of subjacent hypodermis which the lacunar canals traverse. This is followed by layers of transverse and longitudinal muscle fibres.

The proboscis sheath consists of a single layer of muscle fibres in which is embedded, at the posterior end, a big nerve ganglion. This ganglion forms the central nervous system of the worm, with a few nerve retinaculi which go out to supply the body wall.

The male genitalia consist of a pair of testes, a syncitial prostatic gland, a prostatic reservoir, a seminal vesicle, a pair of vasa efferentia, a vas deferens, a muscular penis and a bursa (Fig. 2). The elongated oval testes lie one behind the other about the middle of the body. The two vasa efferentia after running for a short distance swell up, each forming a club-shaped vesicle, and then

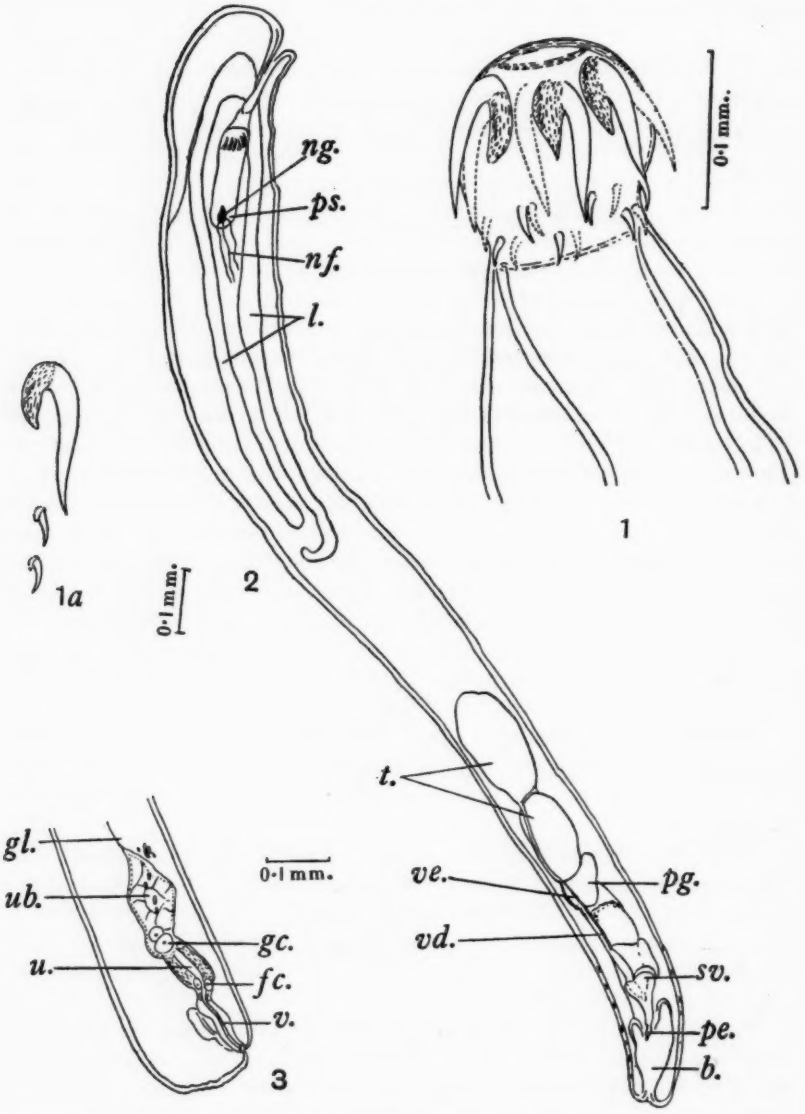

Fig. 1. *Neoechinorhynchus topseyi*. Anterior part showing the proboscis highly magnified. 1 *a*. Side figure shows the hooks of the anterior, middle and basal rows.

Fig. 2. *Neoechinorhynchus topseyi*. Young male specimen showing the genitalia. *b*. bursa; *l*. lemnisci; *nf*. nerve fibres; *ng*. central nerve gland; *pe*. penis; *pg*. prostatic gland; *ps*. proboscis sheath; *sv*. seminal vesicle; *t*. testes; *vd*. vas deferens; *ve*. vas efferens.

Fig. 3. *Neoechinorhynchus topseyi*. Posterior portion of female showing the genitalia. *fc*. flask-shaped cells; *gc*. guard cells; *gl*. genital ligament; *u*. uterus; *ub*. uterine bell; *v*. vagina.

continue to join with each other to form the vas deferens. These vesicles of the vasa efferentia are situated near the level of the prostatic gland. The prostatic gland is a syncitial mass which empties its contents into a reservoir, the prostatic reservoir. This reservoir gives out a duct, the prostatic duct, which ends at the base of the penis. The penis is a muscular cone-shaped organ situated at the top of an eversible bursa. The seminal vesicle is a big thin-walled pouch which narrows posteriorly and opens in the penis. The duct from the vas deferens also opens in the penis along with the duct of the seminal vesicle. The bursa is a funnel-shaped eversible organ which is everted out at the time of mating or with slight pressure.

The female genitalia (Fig. 3) consist of a uterine bell, uterus, vagina and ova. The uterine bell is a thin, funnel-shaped organ attached at the anterior end to a ligament, the genital ligament, which is attached to the base of the proboscis sheath. There are a few cells in the bell, the guard cells which serve to sort out the mature from the immature ova, only allowing the mature ones to pass into the uterus. The uterus is a long flabby tube which opens into the vagina. A couple of flask-shaped cells are present in the uterine wall at the posterior end. The tubular vaginal wall has two sets of strong muscular

Table I. *Showing measurements of closely related species of* Neoechinorhynchus[1]

Species	Dimensions	Proboscis	Proboscis hooks	Subcuticular nuclei
N. agilis (Rudolphi)	♀ 45 × 0·5–0·1	3 rows of 6. Longer than broad	(i) 0·09–0·12 (ii) 0·041–0·053 (iii) 0·03–0·07	Dorsal 4 Ventral 2
N. rutili (Muller)	♂ 2–6 ♀ 5–10	0·038 × 0·019–0·021	—	—
N. australis Van Cleave	♂ 3·5–7·0 ♀ 4–18 × 0·35	0·15–0·18 × 0·12–0·15 3 rows of 6	—	—
N. cylindratus Van Cleave, 1913	♂ 4·5–8·5 × 0·5–0·7 ♀ 10–15 × 0·7	0·172 × 0·15	(i) 0·079–0·097 (ii) 0·037 (iii) 0·021–0·025	—
N. tenellus Van Cleave, 1913	♂ 2–8 ♀ 3·5–13 × 0·6	Cylindrical 0·15 × 0·135	(i) 0·09–0·11 (ii) 0·038 (iii) 0·027	—
N. crassus Van Cleave, 1922	♂ 4–7 ♀ 6–9	0·27–0·325 × 0·24–0·27	(i) 0·094–0·10 (ii) 0·071–0·083 (iii) 0·047–0·071	—
N. magnus Southwell & Macfie, 1915	♀ 90 × 1·5	3 rows of 6	(i) 0·06–0·071 (ii) 0·03–0·037 (iii) 0·018	—
N. variabilis	♂ 9–25 ♀ 7–50	—	—	—
N. zacconis Yamaguti, 1935	♂ 1·43 × 0·037	60 × 48μ	(i) 24μ (ii) 18μ (iii) 12μ	—
N. topseyi n.sp.	♂ 1·30–28·5 × 0·17–1·10 ♀ 7·0–69·0 × 0·50–1·5	0·15 × 0·14	(i) 0·095 (ii) 0·025 (iii) 0·024	Dorsal 5 Ventral 2

[1] All measurements are in millimetres except where otherwise stated.

bands, the vaginal sphincters. The external opening of the genitalia, the vulva, is situated at the postero-ventral end.

Measurements (in mm.): Males 1·30–28·5 × 0·17–1·10; females 7·0–69·0 × 0·50–1·50; proboscis 0·15 × 0·14; proboscis hooks: anterior row 0·095, middle row 0·025, basal row 0·024; proboscis sheath 0·410 × 0·132; lemnisci I, 0·990 × 0·066; II, 0·836 × 0·066; testis anterior 4·861 × 0·220, posterior 4·275 × 0·220; prostatic gland 1·100 × 0·154; prostatic reservoir 0·418 × 0·176; penis 0·154 × 0·099 (at the widest end).

From Table I it is clearly evident that the main points of difference between the various species of *Neoechinorhynchus* and the new species are the size of the body of the male and the female specimens, the size of the hooks, the number of giant subcuticular nuclei and the size of the proboscis.

In the new species *N. topseyi* the males are generally much smaller and more slender than the females; the wall of the proboscis sheath is single layered; the hooks of the anterior row are much longer than the middle and basal rows; the central nervous system is situated near the base of the proboscis sheath; the prostatic gland is a single syncitial mass; subcuticular nuclei are present and the lacunar system is well developed.

Host. *Polynemus heptadactylus* (Cuv. & Val.).

Location. Intestine.

Locality. Calcutta, India.

Type specimens are deposited in the collection of the Zoological Survey of India, Indian Museum, Calcutta.

In conclusion I must express my hearty thanks to Mr M. N. Datta, Zoological Survey of India, Indian Museum, Calcutta, for helping me in identifying the specimens and in the compilation of this paper. I am also indebted to the authorities of the Zoological Survey of India, Calcutta, for the facilities extended to me for my work.

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THE LIFE CYCLE OF *ADELINA CRYPTOCERCI* SP.NOV., A COCCIDIAN PARASITE OF THE ROACH *CRYPTOCERCUS PUNCTULATUS*

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(With Plates XV–XIX, containing Figs. 1–55 and Fig. I in the Text)

Introduction

Adelina cryptocerci is an intracellular parasite in the tissues of *Cryptocercus punctulatus*, a primitive wood-eating roach found in rotten logs in northern California, Oregon, and parts of eastern United States.

The parasite was called to the attention of the author by Dr Harold Kirby, who discovered it in 1931 in some dead roaches in his vivarium. Two years later he found the infection in another lot which had been kept there for 7 months.

Cleveland *et al.* (1934) mention in a footnote that on a few occasions a coccidian of the family Adeleidae had been seen in *Cryptocercus*, sometimes being generally distributed throughout the body. This is probably the species of *Adelina* here described.

In advanced heavy infections the coccidia are to be found in nearly every part of the body: head, antennae, mouth-parts, legs, fat-bodies, salivary glands, muscles, and even within the nerve cord. In earlier, lighter infections the Protozoa are more strictly confined to the fat-bodies around the digestive tract.

The percentage of infection in freshly collected roaches is not high; it is estimated at about 3 per cent in those which have been examined from northern California. Whether it occurs at all in the eastern roaches has not been investigated, and Cleveland does not make any statement as to the locality from which the roaches in which he observed the infection were collected. A much higher percentage of infection than this has been found when a large number of the insects have been kept together for some time, apparently as a result of the roaches' habit of eating their dead companions. Under natural conditions they tend to remain isolated in small groups in their tunnels in the logs which they inhabit, and the chances of a dead one being eaten by many others are not great.

The infection is transmitted by ripe oocysts containing the infective sporozoites, ingested with the tissues of a dead or enfeebled roach. Artificially induced infections can easily be obtained, as the insects readily

seize upon parts of others placed near them and can thus be given a large number of cysts within a short time.

The genus *Adelina* was founded by Hesse in 1911 for a coccidian which he described from the oligochaete *Slavinia appendiculata*. This coccidian, which he named *Adelina octospora*, was placed in a new genus because the sporocysts differed from those of members of the genus *Adelea*, being spherical in shape rather than discoidal as are those of *Adelea*. Several species earlier described as *Adelea* Hesse were then placed in the new genus *Adelina*. Other species that have been described are: *Adelina dimidiata* (Schneider, 1885; Balbiani, 1889; Léger, 1897, 1898; Schellack, 1913), from the intestine of several species of *Scolopendra*; *Adelina simplex*, by Schneider in 1885, from the intestine of *Gyrinus* larvae; *Adelina mesnili*, by Pérez in 1899, in fat-bodies of *Tineola biseliella*; *Adelina tipulae*, by Léger in 1897, in the intestine of *Tipula* larvae; *Adelina akidium*, by Léger in 1900, from the body cavity and intestine of *Akis* and *Olocrates*; *Adelina transita*, by Léger in 1904, from the body cavity of *Embia solieri*; *Adelina zonula*, by Moroff in 1906, from the fat-body of *Blaps mortisaga*; *Adelina* sp., by Chatton in 1912, from the intestine of *Scincus officinalis*; and *Adelina tenebrionis*, by Sautet in 1930, from the body cavity of larvae of *Tenebrio molitor*.

The stages in the life cycle of *Adelina cryptocerci* do not differ greatly from those of other species of *Adelina* which have been described in detail. There are, however, certain questions with regard to sexual differentiation and meiosis which have not as yet been solved in this genus, upon which my findings in *A. cryptocerci* throw some light. Within the family Adeleidae, zygotic meiosis has been found to occur in *Adelea ovata* by Greiner (1921) and in *Klossia helicina* by Naville (1927), but none of the descriptions of species of *Adelina* contains any information concerning meiosis in this genus.

The matter of differentiation of male and female gametes from one haploid organism is one of considerable interest, both as to the time and the manner of its occurrence. Léger & Duboscq (1902) described in *A. dimidiata* two types of schizogony which they considered as forming male and female merozoites respectively. Schellack (1913) does not confirm this dimorphism. Moroff (1906) described three types of schizogony in *A. zonula*: one, occurring early in the infection, in which a large schizont gives rise to 16–40 merozoites; a second, smaller, forming 16–24 merozoites; and a third, occurring only at the time of gametogenesis, in which the nuclei are disposed in two rows, forming two groups of shorter, broader merozoites at the ends of the schizont. Of these Moroff interpreted the second type as the schizogony in which macrogametocytes were formed, the third, that in which microgametocytes were formed. According to Naville (1931), however, among the Adeleidae in every case that has been studied more recently a bipolar arrangement of merozoites is manifested in the course of gametogony. This author considers the bipolar arrangement an indication of sexual polarity, the microgametocytes being formed at one end of the schizont and the macrogametocytes at the other. That this

condition occurs in *A. cryptocerci* and is evidence of a gametogonial division will be shown in the following description.

Material and methods

The roaches used for this work were collected from fallen Douglas firs within a small area near the Smith River in northern California, 20 miles north of Crescent City.

All stages of the parasite except the initial infecting stages can be found in one heavily infected roach. The problem that arises is that of arranging the stages in their true chronology. In order that this might be done with certainty a series of experiments in artificial infection was carried out. Since the incidence of infection was low in freshly collected roaches, and it was impossible to tell without killing an individual whether or not it was already infected, the only recourse was to use a group of roaches which, on examination of a number, showed no infection, and to assume that there would be enough of the rest uninfected to give the sequence of events in the cycle. The presence of ripe and old brown cysts in the tissues was an indication of infection for some time; and if they were found in a roach examined soon after having been fed on mature cysts, they were proof of a pre-existing "natural" infection. Thus it could be determined whether coccidia were already present before experiment.

For determination of the presence and stage of infection small pieces of fat were removed from the body cavity and examined in Ringer's solution for cold-blooded animals. Permanent preparations were made by fixing in warm formol-sublimate, imbedding in paraffin, serial sectioning at 10μ, and staining in Delafield's, Ehrlich's, or iron haematoxylin. Fixing fluids of Bouin, Zenker, Gilson-Carnoy, Flemming, and Schaudinn were also used, but the best results were obtained with formol-sublimate (3 parts mercuric chloride, 1 part formalin). For special cytological studies the fixing fluids of Helly, Régaud, Champy, Hirschler and Nassonov were used.

Experiments in artificial infection

It was at first thought that the roaches obtained the infection from ingestion of cysts with wood contaminated in some way by others having the infection. This idea was based on the fact that roaches collected by Dr Kirby in May showed no infection in the few examined soon after being collected, but one was found dead, heavily infected, the next December after having been kept in the vivarium in which the earlier infected lot had been kept. Later, in February of the same winter, several more infected roaches were found in this vivarium. That these insects did not obtain their infection from the wood, however, was shown by keeping 46 in this tank later in the spring for 2 months, during which time many died, but none was infected with coccidia. From these facts it was concluded that they must become infected with coccidia from each other, and that unless there were infected ones among

them they could live in and eat the wood formerly inhabited by infected individuals and not become infected. If, however, there were even one infected roach in the group, it might serve as a source of infection to many others upon its death and consumption by them. This conclusion led to experiments in feeding coccidia from known infected roaches to groups in which the incidence of infection was found to be low.

In the feeding experiments mature cysts were fed to the experimental roaches by isolating these in groups of 3–5 in Petri dishes with pieces of infected tissue until they had been consumed, when the insects were returned to dishes containing wood or filter paper. Individuals were removed, examined, fixed and sectioned, daily during the first week, every other day during the second week, and approximately every 3 days thereafter until mature cysts were found.

Controls were kept in two ways. First, a group of roaches from the lot used in feeding experiments was kept in one container, thus giving them a chance for contact and for consumption of any that might die. Secondly, 7 groups of 5 each, from the lot used in feeding experiments, were isolated in Petri dishes with moist filter paper. These were watched closely to make sure that no dead were eaten.

The results of these experiments may be briefly summarized. Of 110 roaches examined from 10 hours after feeding to as late as 140 days, 92 (84 per cent) were found to be infected, or in some of those examined soon after feeding, to have sporozoites in the lumen and epithelium of the midgut. Of 35 controls isolated in groups of 5, only 1 (2·8 per cent) was infected, and this was undoubtedly infected before the beginning of the experiment, as shown by the presence of old brown cysts only 35 days after the experiment was begun. Of 35 roaches kept in 2 groups and not observed closely, 22 died and were not examined, 12 were examined and found infected, and 1 was uninfected; so that in these larger groups the infection was over 34 per cent and probably much higher, since the remaining 13—after 22 had died—showed 92 per cent infection.

The serial sections of roaches killed at intervals after feeding furnished adequate material for the determination of the succession of stages in the cycle of the coccidian. These stages are described in detail, and their times of appearance after feeding cysts to the host are given in the following description of the life cycle.

THE LIFE CYCLE

A. *Sequence of stages of infection*

The sequence of stages in the cycle, and their times of appearance, will first be given, after which each stage will be described in detail.

Ripe oocysts are ingested with tissues of dead infected roaches. At 10 hours after ingestion some of the oocyst walls have opened, and many free sporocysts are present in the lumen of the gut. After 24 hours free sporozoites

may be seen moving about in material obtained by squeezing out the contents of the midgut, while in sections they are found as far back as the posterior colon and penetrating the midgut epithelium.

The sporozoites pass through the midgut wall into the fluid surrounding the intestine and thence to the fat and other tissues in all parts of the body, where they increase in size to form schizonts of the first generation.

From 9 to 13 days no sporozoites have been observed except a few scattered in the midgut epithelium. Those which succeed in getting through the wall of the midgut and into tissues in which they can develop are evidently few, for many unsuccessful examinations have been made for these early stages. At 16 days a few developing schizonts have been found, with from 1 to 12 nuclei. At 21 and 22 days more of these multinucleate somatellas are found, but as yet no merozoites have been formed. The apparent increase between the sixteenth and twenty-first days is probably merely the result of increase in size, as young stages are difficult to discern among the cells of the host. Failure to find the sporozoites after they leave the midgut is also doubtless due to their minute size and slight differentiation from the host's cells in staining.

At 25 days bundles containing up to 40 merozoites were present in one roach, as well as many free merozoites that had escaped and small schizonts that were probably of the second generation. The free merozoites were found in various positions and shapes throughout the fatty tissues, as though engaged in active migration at the time of fixation. In the bundles at this time the merozoites were arranged either in barrel-fashion, with a single row of nuclei across the middle, or irregularly.

These merozoites give rise to a second generation of schizonts which produce either similar merozoites or shorter, broader merozoites disposed in a characteristic bipolar arrangement at the two ends of a central residual body. Since the bundles with bipolar arrangement are found only in later infections, at 25–29 days and later, and because their merozoites show characteristic differences from those of unpolarized bundles, it is concluded that the bipolar schizonts are those which give rise to gamete-forming merozoites. These merozoites, which later become distinguishable as of separate sexes, may be called *gametoblasts*, rather than *gametocytes*, which is the term used by Naville, Moroff, Hesse, and others. Since the term *gametocyte* is often used with the implication that a reduction in chromosome number is involved in the ensuing formation of gametes, possible confusion as to the time in the cycle of *Adelina* at which meiosis occurs may thus be avoided.

Gametoblasts of the two sexes can be distinguished when large refractile globules of reserve material appear in the macrogametoblasts. Growth of the macrogametoblast can be traced through forms of increasing size to the large macrogamete in which the cytoplasm is filled with globules. One or two microgametoblasts become attached to the macrogametoblast during its growth, and may be seen flattened against it. As the macrogametoblast attains its full size and becomes rounded the microgametoblast moves to one end,

rounds out, and becomes flattened on the female. At this time both are surrounded by a membrane which may be called the gametocyst, from its homology with the cyst formed round the two gamonts of gregarines. During this time the macrogametoblast nucleus moves from its position near the centre towards one end, where it comes to lie close to the surface. Full-grown associated gametoblasts were found in the fat tissues of roaches 29 days after the feeding of cysts.

The nucleus of the microgametoblast undergoes 2 divisions, forming 4 microgamete-nuclei which become condensed into darkly-staining comma-shaped structures closely applied to the macrogamete surface. The macrogametoblast nucleus shows no evidence of division before fertilization. The term "macrogametoblast" has been adopted for the cell up to the time when it has attained full growth and the microgametes are formed, after which it is referred to as the macrogamete.

One of the 4 microgametes passes through the surface membrane of the macrogamete and fuses with its nucleus. Shortly afterwards a membrane appears round the zygote, pushing away the 3 unused microgametes and the residual microgametoblast cytoplasm and enclosing them between itself and the gametocyst. Later a third membrane is formed, thus completing the formation of a triple cyst wall. Zygotes are formed in artificially infected roaches from the twenty-ninth day onwards.

After certain changes which will be described later, the zygote nucleus undergoes repeated divisions, forming a sporont with from 5 to 21 nuclei, which then breaks up into as many sporoblasts as there are nuclei. Each sporoblast nucleus divides once. After this division sporocysts are formed round the sporoblasts. The nuclei lie superficially in the sporoblast cytoplasm, usually on opposite sides. They become compact, darkly stainable, and are eventually surrounded by an elongate mass of hyaline cytoplasm, leaving a residual group of globules in the centre. Multinucleate sporonts and binucleate sporoblasts are found after 32 days, and mature cysts after 40, following ingestion of infective cysts. This time is somewhat shorter than that observed by Léger (1897) and Schellack (1913) in *Adelina dimidiata*. These authors give the time from successful artificial infection until the appearance of the first cysts in the faeces of the host, *Scolopendra cingulata*, as 55 and 50 days respectively.

The mature cysts remain embedded in the host's tissues until they are liberated in the digestive tract of a second host.

B. *Description of stages*

(1) *Sporozoites.* Sporozoites within the sporocysts are elongate sausage-shaped organisms, in living specimens lying against the cyst wall. Fig. 1 shows a mature oocyst drawn from a smear of fat from a living roach; Fig. 2, 2 sporocysts drawn from sections. Inside the cysts, and for some time after leaving them in the digestive tract, the sporozoites appear in sections to be rounded at the anterior end and to taper gradually to the posterior end. The

nucleus consists of densely packed chromatin granules, has no visible membrane, and appears slightly larger in diameter than the cytoplasm. Within the cysts the sporozoites show a small cone of cytoplasm projecting beyond the nucleus at the posterior end. When they are free in the intestine the nucleus gradually moves forward until it occupies a position approximately in the centre (Figs. 3, 4 and 5). In sections the sporozoites measure 2–3μ in diameter and 15–17μ in length.

Living motile sporozoites were studied in midgut contents 24 hours after ingestion of cysts by the roach. When not moving they taper towards both ends and have a slightly spiral twist (Fig. 6*a*). The cytoplasm is transparent and hyaline except for a few scattered minute granules and small vacuoles. The nucleus occupies the entire width of the sporozoite and is slightly longer than wide. No granules or structures of any kind are visible within the nucleus, but it can be seen clearly because it is more refractile than the cytoplasm. When sporozoites are not in contact with pieces of tissue on the slide they undergo a characteristic movement of bending the two ends until they nearly touch and rapidly extending again to full length. As the bending takes place the more plastic anterior end becomes rounded and thickened. The anterior end rapidly assumes its previous tapering form during the period of extension. Successive forms assumed by a sporozoite during this movement are shown in Fig. 6*a–e*.

If the sporozoite is in contact with cells of the midgut in the preparation it may progress with a screw-like motion, assuming a spiral twist and maintaining a more rigid and constant form, as in Fig. 6*f*. Occasionally one may be observed to attach itself by one end to the slide or a piece of tissue and revolve rapidly in place, as though attempting to bore into the object.

In sections, all stages of the penetration of the epithelium by the sporozoites can be found. The sporozoites may pass between or through the cells, the latter being the method more usually observed. Fig. 7 shows a few midgut cells in section, one of which a sporozoite has penetrated nearly to the base. As in this figure, there is often a definite clear area round the sporozoite, probably resulting from shrinkage in fixation.

Excepting the one shown in Fig. 8 in the muscle layer of the midgut, sporozoites have not been found after leaving the epithelium. This one has enlarged slightly and has either lost its anterior point or is bent so as to appear rounded in this view.

(2) *Schizogony and gametogony.* In experimental infections of *Blaps mortisaga* with *Adelina zonula*, Moroff (1906) was unable to follow the growth of the sporozoite to the first schizont. He assumed that since the sporozoites change into merozoite-like forms their schizogony would be similar to that of the merozoites. Schaudinn (1900) also assumed that in *Eimeria schubergi* and *Cyclospora caryolytica* schizogony of merozoites and sporozoites was similar.

Although the earliest stages in development of schizonts from sporozoites have not been found in *Adelina cryptocerci*, in 16-day infections young schizonts

have been found that are only slightly larger than sporozoites (Fig. 9). Also in these infections larger schizonts are found with 1–4 nuclei (Fig. 10). That they are of the first generation, that is, are developed from sporozoites, is evident because of the absence of merozoites and because of the scarcity of the schizonts. If one period of schizogony had occurred there would undoubtedly be a larger number than has been found.

At 25 days the schizonts have divided into bundles of 8–40 merozoites, the number being proportional to the size of the schizont. They are arranged either barrel-fashion, as in Fig. 17, or irregularly packed together, as in Fig. 12. The merozoites in the two types are identical, and it is thought that the second type of arrangement is merely the result of moving about of the merozoites within the membrane, as they have been observed to do in fresh preparations just before being released. Many free first-generation merozoites are also observed in the 25-day infection, fixed in the act of moving through the fat-cells.

These merozoites are, in sections, 11–13μ long by 2·5–3μ in diameter, tapering toward the two ends. The centrally situated nucleus contains a number of darkly stainable, evenly distributed chromatin granules. At this stage there is no karyosome (Fig. 13).

This first generation of merozoites gives rise to later schizogonic generations. As the merozoites grow into schizonts they become longer and much larger in diameter, reaching eventually a size of 11 by 20μ (Fig. 14). In the mature schizont the cytoplasm is darkly stainable with the haematoxylin stains so that the nucleus is not clearly distinguishable. Small refractile globules are present throughout the cytoplasm except in a small region at each end. In fixed material the globules are dissolved and the cytoplasm has a vacuolated appearance. The nucleus contains a large central karyosome and a more or less distinct circlet of chromatin granules midway between it and the nuclear membrane.

Because of the density of the cytoplasm and its affinity for nuclear stains divisions of the nucleus are difficult to study. In many divisions there seems to be no mitotic figure, but the nucleus has an extended dumb-bell shape, two masses of chromatin finally becoming separated by a constriction between them. Repeated divisions of the daughter nuclei result in the formation of a multinucleate somatella. Occasionally a dividing nucleus is seen which bears more resemblance to a mitotic figure. Fig. 15 shows the anaphase of division of one of the nuclei of a binucleate schizont. In this figure a spindle-like area can be seen between the two poles, with the karyosome lying within it. The chromatin at the poles is in the form of granules and rows of granules, but the chromosomes cannot be counted with certainty. However, many schizonts at a later stage have telophase groups of definite chromosomes which can often be distinguished clearly enough to be counted. The number most often observed is 8. Fig. 16 shows a multinucleate schizont with 7 such groups. When the chromosomes can be clearly distinguished they may often be recognized as of

characteristic sizes: 2 larger, 3 intermediate in size, and 3 smaller. There are 16–32 nuclei in schizonts in which counts have been made.

Each group of chromosomes becomes a clump of indistinctly differentiated chromatin granules surrounded by a nuclear membrane. An elongate portion of cytoplasm around each nucleus becomes separated from the mass, and the bundle of merozoites is formed. Here the arrangement within the bundle may be as in the first generation, with no residual body, or smaller gametoblasts may be formed at the two poles of the schizont, with a large cytoplasmic residual body remaining between the two groups (Figs. 18, 19 and 20). Merozoites from the unpolarized bundles are longer than those of the first generation, but are otherwise similar (Figs. 21 and 22), and grow into another generation of schizonts, thus repeating the cycle indefinitely, as is shown by the presence of merozoites even in the late stages of infection when the host's tissues are packed with mature cysts.

Both the single and the bipolar bundles are surrounded by a definite membrane. Whether this is formed by the schizont or by the host's cells cannot be certainly stated.

One bundle of merozoites similar to that shown in Fig. 18 was under observation when the merozoites began moving about within the membrane; the distinct barrel arrangement became entirely disrupted, and the movements resulted in a rupture of the wall, whereupon 24 merozoites escaped and began to move about actively. In sections bundles are often observed in which the merozoites are arched and irregularly arranged as though moving at the time of fixation.

Living merozoites closely resemble free-swimming sporozoites in structure and movements; they are usually longer, however, being 2·5–3μ by 18–20μ. The nucleus is smaller and not so easily distinguished from the cytoplasm, and the anterior end has not the plasticity of that of the sporozoite. The movements of the merozoites have been described by Pérez (1903) in *Adelina mesnili* and by Moroff (1906) in *A. zonula*.

In fresh preparations the size difference between the merozoites of the single and bipolar bundles appears more clearly than in sections. Figs. 18, 19 and 20 show 3 bundles drawn from living material. Fig. 18 contains the elongate slender merozoites which will form further schizonts, whereas Figs. 19 and 20 show the shorter and broader gametoblasts grouped round a residual body in a more or less bipolar arrangement. Fig. 23 shows in section a group of 32 merozoites with a residual body.

(3) *Sexual differentiation.* Within the bipolar schizonts and in the gametoblasts immediately after their release from the bundles, no differentiation appears that would indicate a sexual dimorphism at this stage. The merozoites are small, 1·5–2·5μ by 9–11·5μ, tapering slightly to blunt ends, with distinct chromatin granules in the oval centrally situated nuclei (Figs. 23 and 24).

Microgametoblasts can be distinguished from macrogametoblasts after some growth has occurred and certain nuclear and cytoplasmic changes have

taken place. In the microgametoblasts one or both ends become sharply pointed. A karyosome, densely staining with iron haematoxylin, appears eccentrically in the nucleus, lying within a clear area outside of which are a number of chromatin granules, the whole being surrounded by a delicate nuclear membrane (Fig. 25).

In the young macrogametoblast the cytoplasm in fixed specimens is highly vacuolated. A small conical projection distinguishes the anterior end from the rounded posterior end. The karyosome is larger than in the microgametoblast, is more nearly central, and is surrounded by fewer chromatin granules (Fig. 26).

In living individuals the young macrogametoblasts are first distinguishable by their large highly refractile globules of reserve substances (Figs. 27 and 57). Living microgametoblasts can be distinguished from merozoites by their more arched form and thicker posterior portion (Fig. 28). Like the merozoites, they are actively motile, moving by doubling the ends together and then extending them. The cytoplasm contains a few refractile granules which are much smaller than those of the macrogametoblast.

That the gametoblasts arise from the shorter merozoites of bipolar arrangement in the schizonts is indicated by the fact that young gametoblasts are shorter than the merozoites produced in schizonts without a residual body, and by the fact that gametoblasts are not present in artificially infected roaches until the bipolar schizonts are present.

That one schizont gives rise to gametoblasts of both sexes rather than that two schizonts give rise independently to the two sexes is indicated by the occurrence in isolated groups of developing micro- and macrogametoblasts in approximately equal numbers in artificial infections in which the infection has not been running sufficiently long to have produced the mixed condition of all stages that is found in old infections. Such groups of gametoblasts are found with no other Protozoa near them, and all of one group are concentrated within a few adjacent host cells. It is unlikely that in all these cases one microgametoblast-producing schizont and one macrogametoblast-producing schizont would develop together in close proximity so that their gametoblasts when liberated would become mixed together.

(4) *Formation of microgametes.* The microgametoblast does not change markedly between the time when it can first be distinguished from undifferentiated merozoites and macrogametoblasts and the time of its attachment to the macrogametoblast. After it becomes attached to the side of the macrogametoblast it retains its elongate form, being somewhat longer and greater in diameter than the early gametoblasts (Fig. 32). The nucleus remains central in position and still shows a karyosome and surrounding chromatin granules. As the macrogametoblast matures, the nucleus of the microgametoblast loses its karyosome, the gametocyst or membrane surrounding the two gametoblasts appears, and the microgametoblast usually moves to one end of the macrogametoblast, where it rounds out and becomes more

closely applied (Figs. 34 and 56). This migration of the microgametoblast may fail to occur, and mature associated gametes are occasionally seen in which the attachment is lateral (Fig. 36) or in which one microgametoblast has moved to the end while a second has remained on the side.

Before division of the nucleus of the microgametoblast the chromatin granules are condensed into a more compact mass. The 2 divisions resulting in formation of 4 microgametes show, like many schizogonic divisions, no sign of spindles, asters, or centrosomes. The nucleus simply elongates into an irregular mass in which dark chromatin granules can be seen in a lighter matrix (Fig. 35). A constriction divides the mass into 2 parts, each of which undergoes a similar division to form 4 microgamete nuclei. Greiner (1921) describes a similar division in formation of microgametes in *Adelea ovata*, without evidence of chromosomes until after the second division. In *Adelina cryptocerci* the chromatin appears to be in the form of chromosomes after the last division (Fig. 36), but these are so closely grouped that attempts to count them have not been successful. In each nucleus the chromatin becomes more closely packed together until a homogeneous, darkly staining, triangular or comma-shaped microgamete is formed which measures about 2·5 by 3μ (Figs. 37 and 38). If attachment of the microgametoblast is at the pole opposite the macrogamete nucleus, 1 or 2 microgametes may migrate to the other end of the macrogamete.

One of the microgametes enters the macrogamete and fuses with its nucleus. The 3 others remain outside and are often seen in a group between the gametocyst and oocyst walls. Often a bulge between the two indicates the presence of the cytoplasmic residuum of the microgametoblast.

(5) *Formation of macrogametes.* The macrogametoblasts grow enormously during their development and are extremely variable in size, being 20 by 25μ to 46 by 51μ when fully grown. During growth many changes occur in the form of the cell, in its cytoplasmic make-up, and in its nuclear structure.

During the earlier part of the growth period the macrogametoblast retains approximately the same shape as that of the young one: an elongate form, rounded posteriorly, with a short, conical protuberance on the anterior end. To judge from their positions in fixed tissues they move little during growth, sister cells from one bipolar division remaining in a localized group in the host's tissue. As the macrogametoblast becomes larger it loses the anterior process and becomes oval.

In the youngest living macrogametoblasts only fine granules and large refractile globules can be observed in the cytoplasm (Figs. 27 and 29). As it increases in size smaller globules appear among the large ones (Fig. 31). In the fully grown gametoblast a layer of large globules lies just under a hyaline layer immediately beneath the surface membrane, and the smaller globules fill the space between this layer and the nucleus (Fig. 34). The larger globules at the periphery are stained red in Helly-fixed material that has been stained by Altmann's mitochondrial method; and with Hirschler's and Nassonov's

methods for Golgi material (Bowen, 1928) they are blackened both in young and in full-grown gametoblasts. These staining reactions indicate the lipoidal nature of these globules, and their distribution in the mature gametoblast corresponds with that of the lipoids and fats described by Joyet-Lavergne (1926) in *A. dimidiata*.

In preparations fixed in 100 per cent alcohol, stained with Lugol's solution, and dehydrated in acetone and toluene according to directions of Joyet-Lavergne (1926) for demonstrating paraglycogen, the smaller globules between nucleus and periphery in large gametoblasts were stained a pinkish brown colour, while the peripheral region remained unstained. This distribution also corresponds with Joyet-Lavergne's description of that of paraglycogen in mature macrogametes of *A. dimidiata*.

In Helly- and Régaud-fixed tissues stained by Altmann's mitochondrial method small granules and rods appear in the young gametoblast around the periphery and among the vacuoles left by dissolving of the large lipoid globules, which at this stage are not stained by this method (Fig. 30*a*).

In tissues and smears fixed according to Hirschler and Nassonov (Bowen, 1928) for Golgi bodies, many fine rods and granules and dumb-bell-shaped bodies in the large gametoblasts are blackened. These have the appearance of chondriosomes but do not have the same distribution as the Altmann-stained rods and granules; they are most numerous round the nuclear membrane and are found in smaller numbers evenly scattered through the cytoplasm among the larger globules.

The distribution of cytoplasmic elements in the full-grown macrogamete may be summarized as follows: chondriosomes peripherally situated, close to the surface; large globules of a lipoid nature in a layer under the chondriosomes; smaller paraglycogen globules between the nucleus and the layer of lipoid globules; and Golgi material in the form of fine granules and rods round the nucleus and among the paraglycogen bodies.

Early in the growth of the macrogametoblast the circlet of chromatin granules round the karyosome becomes more distinct. Sometimes it appears as a halo completely surrounding the karyosome, about equidistant between it and the nuclear membrane, but more often the karyosome lies eccentrically (Fig. 30). As growth continues a vacuole often appears beside the karyosome within the circlet of granules (Fig. 32). The granules become again less clearly stainable and less concentrated as growth progresses, finally disappearing before the nucleus moves to one end of the cell, and leaving only a cloudy mass around the karyosome (Fig. 33). In the full-grown macrogamete the nuclear membrane is indented by the vacuoles around it, and no nuclear structures are visible except the large darkly-staining karyosome, which lies near the centre, and 1–3 small lightly-staining spheres of which 1 or 2 sometimes rest on the karyosome (Figs. 35 and 38). In living macrogametes a light area among the globules indicates the position of the nucleus and no intranuclear structure is discernible.

Shortly before entrance of the microgamete the macrogamete nucleus becomes flattened against the end of the cell. There is no indication at any time of nuclear divisions of the macrogamete before fertilization, and therefore no basis for supposing that there is a gametic reduction in chromosome number.

(6) *Fertilization and resulting zygote.* Penetration of the macrogamete by a microgamete, and the dispersion of the latter within the nucleus of the former, apparently occupy only a brief time. In the many cysts examined, actual entrance of the microgamete has been observed only twice. In both instances the macrogamete nucleus was flattened into a spindle-shaped vesicle at one end of the cell, and the microgamete lay in the cytoplasm at one end of this nucleus (Fig. 39). The macrogamete nucleus contained no karyosome, although in the last stage observed before this a large karyosome was present (Fig. 38). Shortly after entrance of the microgamete a membrane appears on the surface of the macrogamete, separating the remaining microgametes and the microgametoblast residuum from the zygote and enclosing them between itself and the gametocyst. Thus a double cyst wall is formed which is clearly visible in fresh material (Fig. 58), often showing a thickening where the microgametoblast residuum lies.

After formation of this membrane, which may be called the first oocyst membrane, the synkaryon is seen as a spherical vesicular nucleus lying between the periphery and the centre of the zygote. In three instances in which the synkaryon lay near the periphery a distinctly stained group of granules could be discerned within it, the rest of the nucleus remaining lightly stainable (Fig. 40). This group of granules is interpreted as the chromatin of the microgamete. As the zygote nucleus moves towards the centre the granules become dispersed and more numerous and a linin mesh appears, the additional granules and the linin mesh presumably arising from the macrogamete nucleus itself (Fig. 41).

The next stage shows a distinct third membrane, the second oocyst membrane, around the zygote (Fig. 42). Whereas the first two membranes remain together as a uniformly oval double cyst wall except at the place or places where they are separated by the microgametoblast remnant and unused microgametes, this third membrane lies in folds over the surface of the zygote, which shrinks during fixation. The double cyst wall and the second oocyst membrane can be distinguished at all later stages in fixed and sectioned material. The nucleus, still near the centre, is sometimes a crowded mass of chromatin granules, at other times a tangle of fine threads (Fig. 42). The chromatin threads eventually shorten and become thicker, and the nucleus again moves nearer to the surface of the zygote (Fig. 43). At all times, however, the threads are too numerous and tangled to permit of counting or distinguishing as separate entities.

One zygote has been found in which the nucleus appears to contain 8 pairs of granules (Fig. 44). These pairs seem to be homologous macro- and microgamete chromosomes, and the preceding stages in which tangled threads appear

in the synkaryon correspond to premeiotic stages during which the chromosomes become paired and shortened in preparation for segregation during chromosomal reduction. After this stage in which the chromosomes can be distinguished, however, they become again indistinguishable as a long spindle is formed parallel to the surface of the zygote (Fig. 45). Although many zygotes have been observed with such spindles, in no case could chromosomes be distinguished as anything but long threads polarized at the ends of the spindle, but in too indistinct and tangled a mass to be counted.

(7) *Sporogony.* Although many zygotes are found in which the first division of the synkaryon appears to lie in an arrested anaphase, actual separation of the two poles has not been observed. In the later sporont divisions, as in those of schizonts and microgametoblasts, the chromatin net often seems to pull apart into two masses which may show strands extending towards the region of constriction (Fig. 48). In several sporonts, however, figures resembling the anaphase of a true mitotic division have been observed, in which there is a group of granules and 2 or 3 long chromosomes at each pole, but no centrosomes or spindles (Fig. 46). The granules probably represent the smaller chromosomes. They are too crowded and indistinct to permit accurate counts to be made, but the total number at each pole is certainly several less than 16 and therefore doubtless the haploid number.

After the division is completed, in the telophase nuclei distinct chromatin clumps appear. There may be 8–10 distinct granules, or a larger variable number of smaller and less clearly defined particles. In a few cases the granules seem to be arranged definitely in pairs. Fig. 47 shows a nucleus from an 8-nucleate sporont in which 7 pairs of rods and granules and 1 larger single element are distinguishable. If these granules and rods are chromosomes, either the reduction division has not yet occurred at this stage, or an early doubling of chromosomes for the ensuing division has already taken place. Since the anaphases of sporogonial divisions give evidence of a haploid chromosome number, the latter interpretation is probably correct. In nuclei in which larger numbers of less distinct chromatin granules occur it is probable that the chromosomes have broken down into parts in formation of interphase nuclei, which frequently show a large number of small chromatin bodies.

In sporogonial divisions the nuclei always lie near the surface. When the divisions are completed each nucleus lies in a cytoplasmic elevation. By cytoplasmic fission the sporont divides into as many spherical sporoblasts as there are nuclei (Fig. 49), leaving no residual cytoplasmic body, although a few large refractile globules are often seen floating in the fluid of mature cysts, outside the sporocysts (Fig. 1).

Within each sporoblast the nucleus lies at the surface and consists of a mass of chromatin granules which are inconstant in form and number and are not surrounded by a membrane. Each sporoblast nucleus divides once. As in the other divisions, no true mitotic figure is seen, the granules being merely separated into two groups. Long, darkly-staining strings of chromatin some-

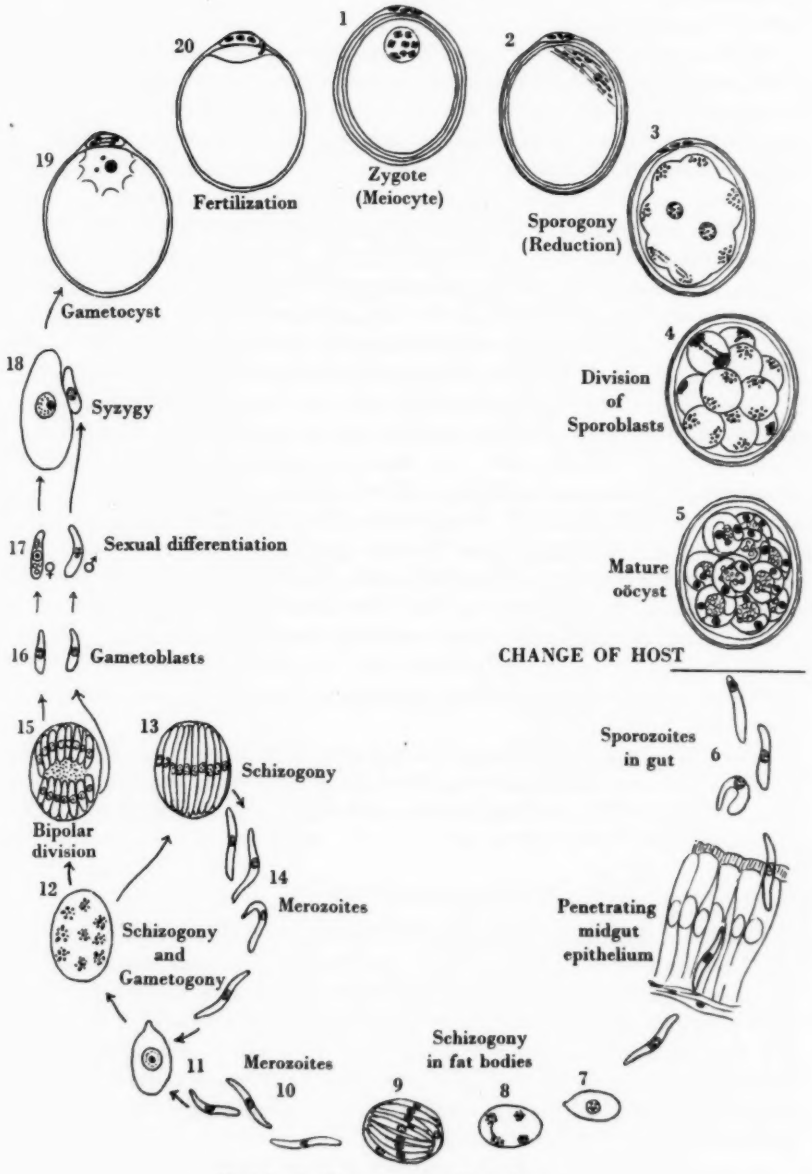
times remain between the two daughter nuclei after they have moved to opposite sides of the sporoblast, as shown in one sporoblast of Fig. 50. In the telophase, however, chromosomes can be distinguished. There are characteristically 8, of constant sizes and shapes. Many nuclei show 10 or more granules, but some of these probably result from chromosomes breaking down during reconstruction of the interphase nuclei, as in nuclei of the sporont. Fig. 50 shows a number of sporoblasts during and after division; Fig. 51, sporoblasts in telophase; and Fig. 54, after telophase, with nuclei in various stages of reconstruction. The lower sporoblast in Fig. 54 contains 2 small darkly-staining nuclei similar to those of fully formed sporozoites. These small dark nuclei, usually lying opposite each other in the sporoblast, become surrounded with hyaline cytoplasm which is eventually separated off into the elongate sausage-shaped sporozoites, with nuclei first centrally, later posteriorly, situated (Figs. 2 and 55). The cytoplasmic globules are left in the centre; they disappear during fixation and are seen only in living cysts, where they are so numerous as to obscure the sporozoites, as can be seen in Fig. 1. Sporocyst walls are formed between the time of division of the sporoblast nuclei and formation of sporozoites. Both in living cysts and in sections the sporocyst wall appears as a double line, but since the two parts remain uniformly close together they probably represent the two surfaces of a membrane of some thickness rather than a double cyst (Fig. 2). The second oocyst membrane shows in sections a similar structure.

Sporocysts vary from 10 to 12μ in diameter. The size of the oocyst varies with the number of sporocysts that it contains. In 25 oocysts, sizes varied from one 24 by 28μ containing 5 sporocysts to one 46 by 51μ containing 21 sporocysts. The average for the group was 31·6 by 40·9μ, and the average number of sporocysts in 31 oocysts in which counts were made was 10·4.

C. *Discussion of the life cycle*

The cycle of the protozoon may now be considered in its entirety. Referring to the diagram in Text-fig. I, the genetic individual originates with the formation of the zygote at 1, and may increase indefinitely by asexual reproduction, which occurs in sporogony (2–5), schizogony (9, 13), and gametogony (15).

The cycle is a haploid cycle and the protozoon may therefore be called a haplont. There is then no chromosomal reduction during gamete formation, and the zygote formed by fusion of the gametes has the diploid number of chromosomes, which is 16. The appearance of tangled threads and of paired granules in the zygote nucleus indicates the occurrence of premeiotic stages in the zygote. Reduction to the haploid number of 8 chromosomes occurs during sporogony, probably at the first division of the zygote nucleus. Using the general cytological term *meiocyte* with reference to the cell in which meiosis is initiated, the zygote is then the meiocyte in *Adelina cryptocerci*, as is the case in *Adelea ovata* as shown by Greiner (1921), and in *Klossia helicina* as shown by Naville (1927). This is in contrast to the condition in many gregarines and in



Text-fig. I. Diagram of the life cycle.

higher animals, in which the meiocytes are the gametocytes. Reduction in the Sporozoa has been discussed at length by Naville (1931) and need not be further reviewed here.

There is no indication of sexual differentiation before the second schizogonial generation, in which gametoblasts of both sexes are formed by a bipolar division of a single schizont. Evidence of actual sexual polarity in the Coccidiomorpha has been furnished by Joyet-Lavergne (1926). This author finds in the merozoites of *Adelina dimidiata* a bipolar distribution of cytoplasmic constituents, of such a nature that the schizont contains in the anterior end the constituents characteristic of the male gamete-forming cells: an important mitochondrial group, little paraglycogen, and a small quantity of reserve lipoids. In the posterior end of each merozoite, and therefore subsequently of each schizont, Joyet-Lavergne finds little chondriome, many paraglycogen granules, and a large quantity of reserve lipoids, all characteristic constituents of the female gamete. Thus even in the merozoite a sexual polarity is detectable. In the bipolar division of the schizont the two sets of characteristics are segregated. Cytological studies of the schizonts at the actual time of this segregation have not been made, but there is proof that gametocytes of both sexes are formed from a single cell in *Klossia helicina*, in which Naville (1927) has found that one schizont undergoes two divisions to form four cells, of which one forms a macrogamete, another microgametes, and the other two may or may not remain undifferentiated. In *Adelina cryptocerci*, although the difference is not detectable at the time of division, the occurrence of macro- and microgametoblasts together in isolated groups indicates their common origin from single schizonts. Growth and the appearance of food reserve globules in the macrogametoblasts differentiate them from the microgametoblasts.

The macrogametoblast forms a single macrogamete, whereas the microgametoblast forms 4 microgametes. One of these enters the macrogamete and fuses with its nucleus, restoring in the resulting zygote the diploid number of chromosomes.

Effect on the host

Just what determines the point at which an infection of *Adelina* becomes lethal to the host is difficult to say. In some roaches that were killed for examination, although the fatty tissue was packed with the parasites and there were many floating free in the body fluids as well as embedded in muscles and other tissues, still the hosts seemed to be healthy and normal. It is probable that there is no exact point at which the infection causes death, but that when the host's tissues are so filled with the parasites there is no adequate defence against certain other causes of death.

If the infection is not too heavy the roach can apparently overcome it in time. In heavy infections many oocysts from the fat bodies are seen which have thick brown walls, the walls often being so dark as to obscure the contents.

Other brown bodies are observed which no longer resemble oocysts, but have the same brown colour. In sections these brown oocysts are dense, while smaller brown bodies are found with closely packed host tissue around them, walling them off. One roach was observed with only the small brown bodies in the fat, as though all the cysts present had been absorbed. In artificially infected insects this could hardly occur to all cysts present, for they become so numerous that it would be an impossibility. As the infection progresses, however, more and more cysts become brown and reduced in size, the depth of colour increasing with decrease in size. Photomicrographs not being printed. Moroff (1906) states that a yellow shell is secreted by dead individuals of *A. zonula*. That the brown substance is produced by the host's tissue is more probable, for in *A. cryptocerci* brown walls are often seen on cysts in which the parasites do not appear to be dead. Rietschel (1935) has likewise come to this conclusion with regard to the brown covering of a possible subspecies of *A. tenebrionis* Sautet, since in the same host a similar brown substance is found around the very distantly related parasites of the genus *Sporomyxa*. The substance would seem therefore to be produced by the host rather than by the parasite.

That any sort of immunity to the coccidian infection is acquired by the roach is doubtful. In one previously infected individual, examined 24 hours after mature cysts were fed, sporozoites were found free in the midgut and moving about actively. In another, with an advanced infection, sporozoites were found in sections in the midgut epithelium 48 hours after cysts were ingested, showing that there was no protection against invasion.

SUMMARY

1. The occurrence of *Adelina cryptocerci* in the host, *Cryptocercus punctulatus*, and its probable means of natural transmission are discussed.

2. Artificial infection experiments were carried out and furnished material for determination of succession of stages in the life cycle of the organism. The cycle is briefly as follows:

(*a*) Mature cysts are ingested by the hosts with tissues of infected roaches. Sporozoites enter the host's tissues by passing through the midgut wall.

(*b*) The first schizogony, in which merozoites are produced, occurs in the fat-bodies between the sixteenth and twenty-fifth days after ingestion of cysts.

(*c*) In the second schizogonial generation two types of schizogony produce merozoites and gametoblasts, respectively, between the twenty-fifth and twenty-ninth days following infection. There is evidence that both male and female gametoblasts are formed from a single schizont.

(*d*) Male and female gametoblasts become associated during the growth period of the latter. When fully grown, they are surrounded by a membrane,

the gametocyst. The male gametoblast undergoes 2 divisions, forming 4 microgametes, of which 1 fertilizes the macrogamete and the other 3 lie unused between the gametocyst and the first oocyst, which is formed shortly after fertilization. A second oocyst is formed before the first division of the synkaryon.

(*e*) By repeated divisions of the synkaryon a multinucleate sporont is formed. This divides into uninucleate sporoblasts. Each sporoblast divides once, forming a sporocyst containing 2 sporozoites. Mature cysts occurred in experimentally infected roaches from 40 days onwards.

3. The stages in the life cycle are described in detail.
4. Evidence for zygotic meiosis in *Adelina cryptocerci* is presented.
5. The effect of the parasite on the host is discussed.

This investigation has been made at the suggestion of Dr Harold Kirby, Jr., and under his direction and that of Dr C. A. Kofoid. I wish to express here my grateful appreciation to both for their interest and many valuable suggestions and criticisms.

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EXPLANATION OF PLATES XV–XIX.

All drawings were made with the aid of a camera lucida. The magnification is 1550 diameters in all drawings except Figs. 16, 47 and 53, in which it is 1890 diameters.

Unless otherwise stated, all figures were made from sectioned material which was fixed in formol-sublimate and stained in Delafield's or Ehrlich's haematoxylin.

PLATE XV

Fig. 1. Mature oocyst containing 11 sporocysts, in each of which are shown 2 sporozoites partially obscured by fat globules. Living, from smear of fat-body.

Fig. 2. Two sporocysts, showing the sporozoites.

Figs. 3, 4 and 5. Sporozoites free in midgut. Fig. 3 shows nucleus at posterior end; Figs. 4 and 5, nucleus migrating towards centre.

Fig. 6. *a–e*, successive stages observed during bending movement of sporozoite in smear of midgut contents; *f*, form assumed in progressive spiral movement.

Fig. 7. Section of midgut wall showing sporozoite in base of epithelial cell.

Fig. 8. Sporozoite in muscle layer of midgut wall.

Figs. 9, 10 and 11. Uninucleate, quadrinucleate, and sex-nucleate schizonts in fat; developed from sporozoites, 16 days after ingestion of mature cysts.

PLATE XVI

Fig. 12. Bundle of first-generation merozoites from the fat-body, 25 days after ingestion of mature cysts.

Fig. 13. First-generation merozoite.

Fig. 14. Later schizont which has developed from a merozoite, showing the large central karyosome and ring of chromatin granules.

Fig. 15. Schizont showing anaphase of nuclear division. The karyosome is seen within the spindle. Two other nuclei are present at a lower focal level.

Fig. 16. Multinucleate schizont showing telophase groups of chromosomes, 8 in each group.

Figs. 17 and 18. Bundles of merozoites arranged barrel-fashion. Fig. 17, Gilson-Carnoy fixation, Feulgen's stain. Fig. 18, living material.

Figs. 19 and 20. Bipolar division. Fig. 19 shows merozoites arranged in radial grouping around residual body. Fig. 20 shows merozoites polarized at the two ends.

Figs. 21 and 22. Merozoites. Fig. 21 shows positions assumed by a living motile merozoite.

Fig. 23. Bipolar division.

Fig. 24. Young undifferentiated gametoblasts.

Fig. 25. Young microgametoblasts. Iron haematoxylin.

Figs. 26 and 27. Young macrogametoblasts. Fig. 27, living.

Fig. 28. Microgametoblast; living, before attachment.

PLATE XVII

Figs. 29, 30, 30*a* and 31. Growing macrogametoblasts. Figs. 29 and 31, living: Fig. 30*a*, Régaud fixation, Altmann's mitochondrial stain.

Figs. 32 and 33. Micro- and macrogametoblasts in association. In Fig. 33 the chromatin granules in the nucleus of the macrogametoblast have disappeared, and the nucleus has moved towards one end.

Fig. 34. Large macrogametoblast with 2 associated microgametoblasts. The gametocyst has formed round the associated gametoblasts. Living.

Fig. 35. Associated gametoblasts. Nucleus of microgametoblast undergoing first division. Iron haematoxylin.

Fig. 36. Associated gametoblasts. Microgametoblast shows 4 nuclei.

Fig. 36*a*. Large macrogametoblast, showing lipoid globules and peripheral mitochondria. Helly fixation, Altmann's mitochondrial stain.

Fig. 37. Microgamete. Iron haematoxylin.

PLATE XVIII

Fig. 38. Mature gametes. Four microgametes flattened between the gametocyst wall and the macrogamete. Iron haematoxylin.

Fig. 39. Fertilization. One microgamete has entered the nucleus of the macrogamete. The other 3 are seen within the gametocyst.

Fig. 40. Granules of the microgamete nucleus becoming dispersed within the nucleus of the macrogamete.

Fig. 41. Zygote. Nucleus shows granules dispersed on a linin net. The first oocyst membrane has formed.

Fig. 42. Zygote. Nucleus shows a tangled mass of chromatin threads. The second oocyst membrane has formed.

Fig. 43. Zygote. Nucleus shows short threads and granules.

Fig. 44. Zygote. Nucleus shows 8 pairs of granules.

Fig. 45. Zygote, showing spindle of first cleavage.

Fig. 46. Anaphase figures in divisions of sporont nuclei.

Fig. 47. Group of chromatin granules from a nucleus of a 12-nucleate sporont. Iron haematoxylin.

Fig. 48. Multinucleate sporont.

PLATE XIX

Fig. 49. Oocyst containing uninucleate sporoblasts. Iron haematoxylin.

Fig. 50. Oocyst containing binucleate sporoblasts. One shows 2 nuclei in anaphase.

Fig. 51. Oocyst containing sporoblasts in telophase. In some of the groups 8 chromosomes are distinguishable.

Fig. 52. Single sporoblast in section. Eight chromosomes are distinguishable in the nucleus.

Fig. 53. Four telophase groups of chromosomes, with characteristic sizes and shapes. Iron haematoxylin.

Fig. 54. Oocyst containing binucleate sporoblasts in various stages of nuclear reconstruction.

Fig. 55. Sporocyst. Sporozoites are being formed by concentration of cytoplasm around the 2 nuclei.

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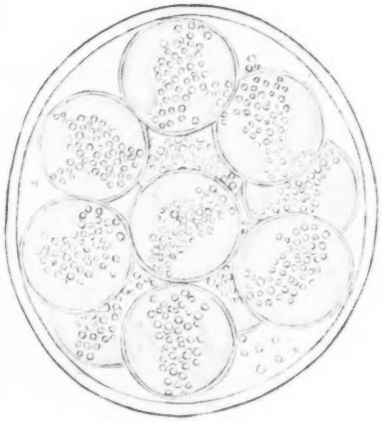

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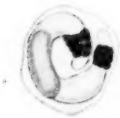

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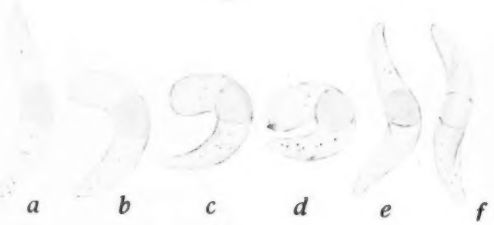

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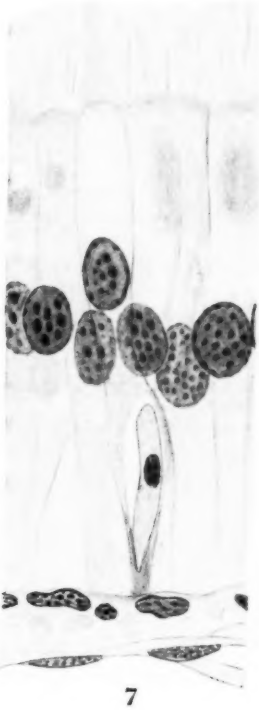

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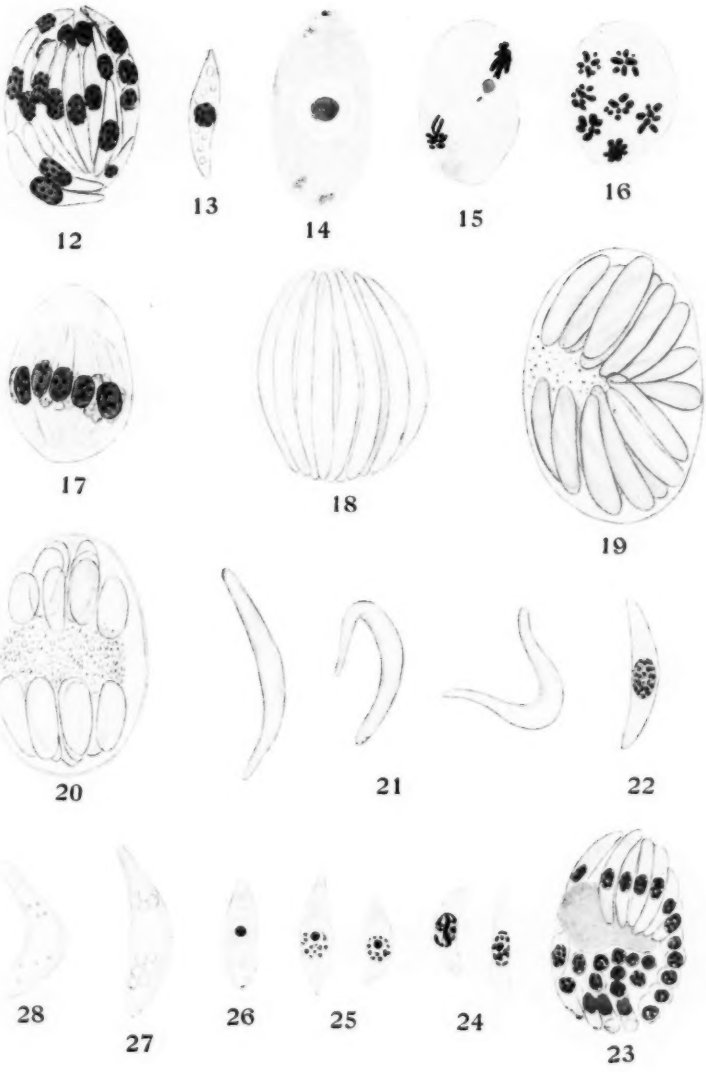

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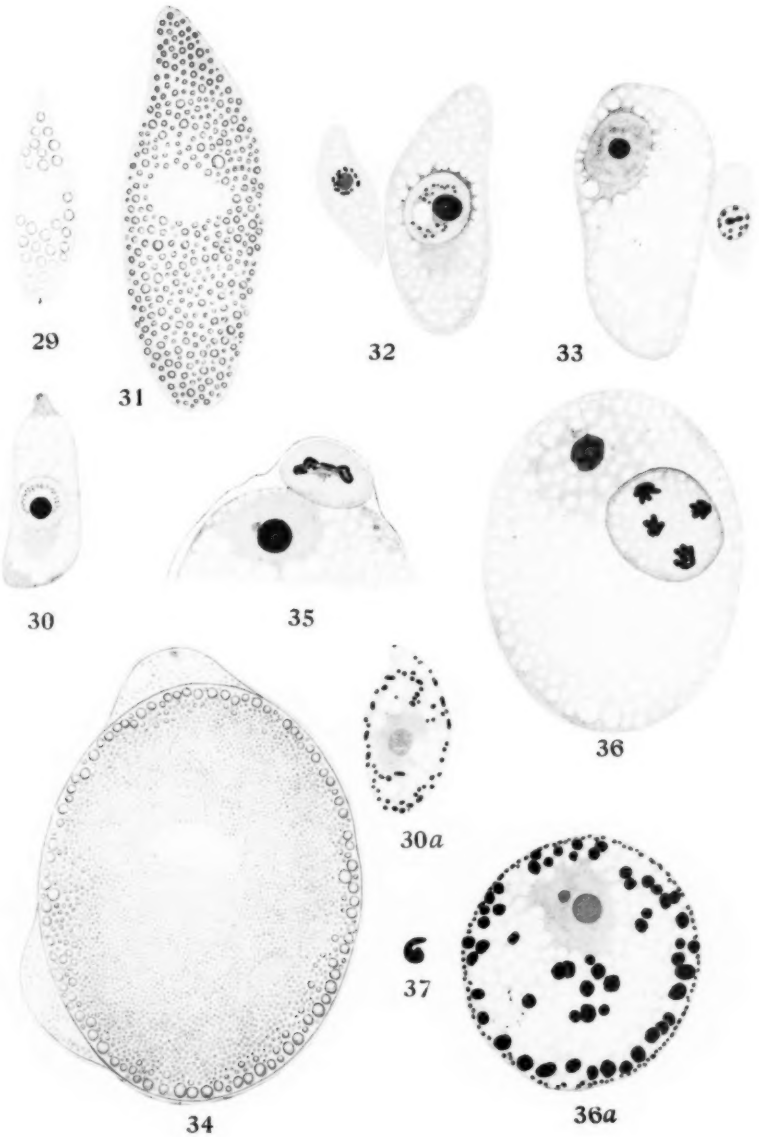

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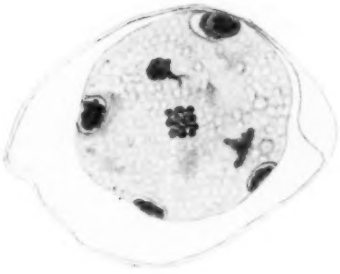

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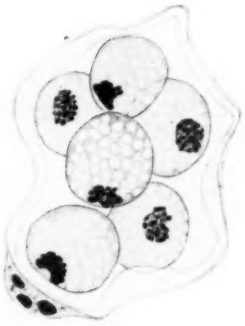

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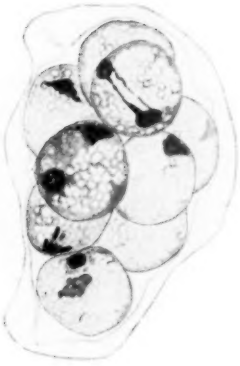

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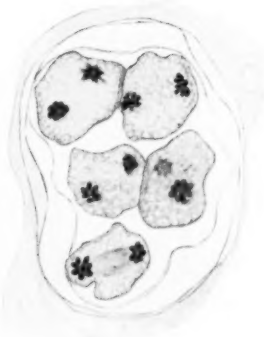

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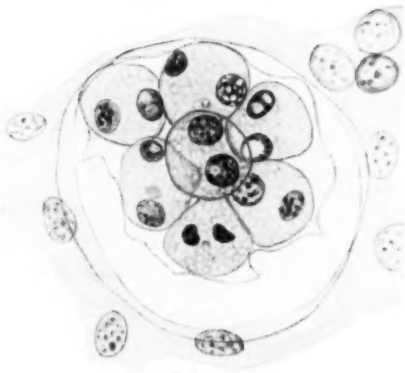

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BADROULBOUDOUR SPLENDIDA N.G. ET SP., A NEW PARASITIC ISOPOD FROM ECUADOR

By W. HAROLD LEIGH-SHARPE, M.Sc. (Lond.)

(With 4 Figures in the Text)

Habitat and record. I am much indebted to Miss Miriam Rothschild for kindly presenting me with a female specimen of a new cymothoid isopod taken from the mouth of a fish known locally as *Boca-Chica*, which, in the words of the collector, is "slightly larger than a herring, scaled, and with a sucker-like mouth", probably a loricariid, from Rio Napo, Ecuador.

Body. The total length of the animal is 2·1 cm. The head is a true cephalothorax, the first thoracic segment being fused with the cephalon. There are seven free thoracic segments of which the first is the longest and narrowest and forms a collar in which in other genera the cephalothorax is immersed. The thorax is widest in the region of the third free segment and tapers posteriorly. The abdomen consists of five segments, four free and one fused with the telson which is as broad as it is long. The eyes are barely visible in dorsal aspect (Fig. 1).

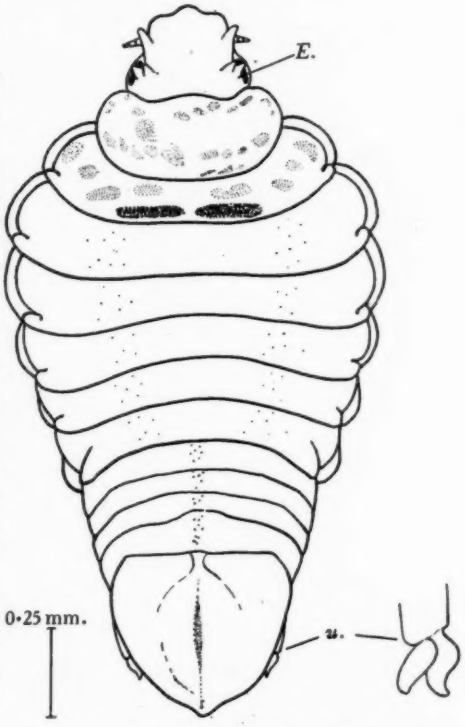

Fig. 1. *Badroulboudour splendida* ♀. Entire animal in dorsal aspect. *E.* eyes; *u.* uropods.

Colour (in alcohol): a pale straw tint; on the first and second free thoracic segments dorsally are roughened patches of dark brown denticles, and on the second segment two larger areas of black denticles represented in the figure by light and dark stippling respectively (Fig. 1). There are minute black pigment spots, on the antennules and antennae (Fig. 4), sporadic in the thoracic region, and in the mid-abdominal and mid-telson regions (Fig. 1).

A brood-pouch (*B*, Fig. 2) is present, formed from the five pairs of epipodites of the free thoracic segments.

The most characteristic feature of the genus, and which occurs in no other, is that the *cephalothorax* stands boldly out from the collar (Fig. 1), and ends anteriorly in three very large, dark brown, prominent, rounded, down-curved

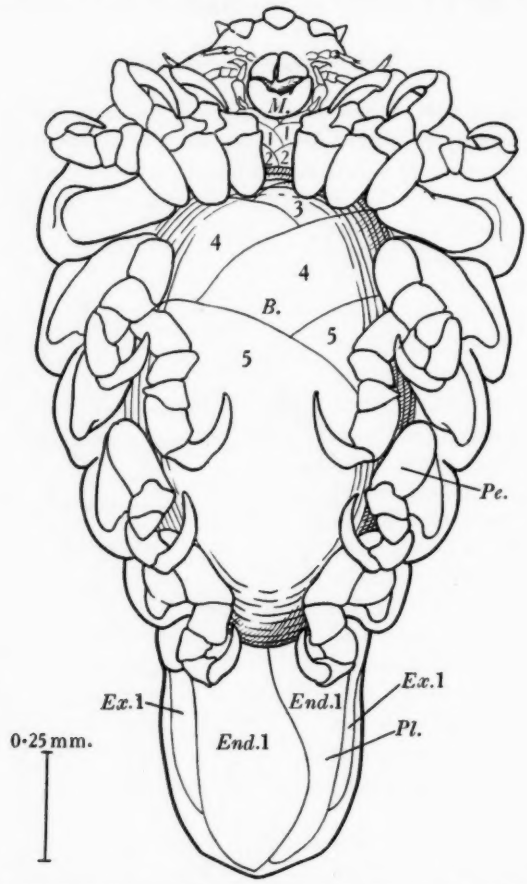

Fig. 2. *Badroulboudour splendida* ♀. Entire animal in ventral aspect. *M.* mouth; 1–5 epipodites; *B.* brood-pouch; *Pe.* pereiopods; *Pl.* pleopods; *Ex.* 1 and *End.* 1 exopodites and endopodites of first pair of pleopods.

bosses, and three pairs of lateral horns (Figs. 1 and 3), one large pair behind the bosses and two small pairs above the eyes dorsally.

Appendages (Fig. 4). *Antennules:* standing well out, four-articled, the apical the largest ending in two setae.

Antennae: seven-articled, the apical very small.

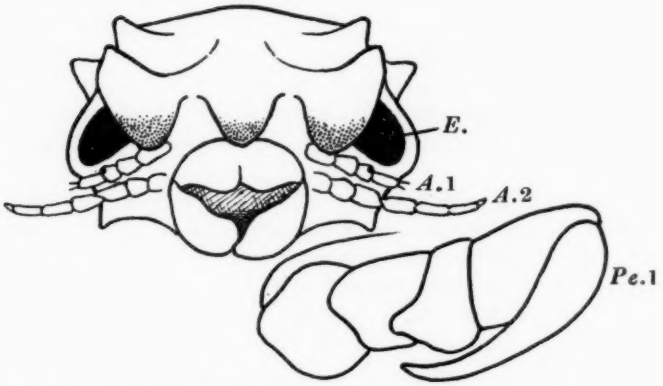

Fig. 3. *Badroulboudour splendida* ♀. Head in anterior aspect. *E.* eye; *A.*1 antennules; *A.*2 antennae; *Pe.*1 first pereiopod.

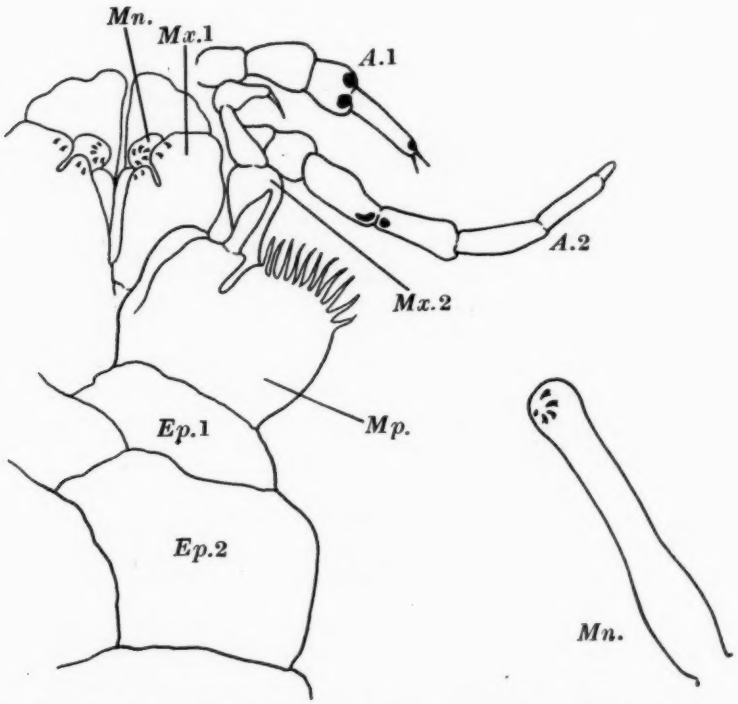

Fig. 4. *Badroulboudour splendida* ♀. Mouthparts in ventral aspect. *A.*1 antennule; *A.*2 antenna; *Mn.* mandible; *Mx.*1 first maxilla; *Mx.*2 second maxilla; *Mp.* maxillipede; *Ep.* epipodite.

Mandibles: rod-like, stout, rounded apically with about five curved denticles.

First maxillae: biramose, of flat plates, denticled.

Second maxillae: apparently uniramose, four-articled.

Maxillipedes: biramose, flattened, the endopodite with an apical article, and the exopodite strongly fringed with setae. The basal portions are fused to form a lower lip.

There are seven pairs of *pereiopods* (Fig. 2), three pairs directed forwards and four pairs directed backwards. Each is five-articled and ends in a simple claw. There are four pairs of *pleopods* (Fig. 2) of which both exopodites and endopodites are modified into flat respiratory laminae, and all are covered in ventral aspect by the first pair.

The *uropods* are small, three-quarters the length of the telson, completely covered in ventral aspect (Fig. 2), and barely visible in dorsal aspect (Fig. 1). The exopodite is the larger, curved outwards apically, and enlarged proximally, the endopodite is of more uniform diameter. They are characteristic of the genus.

Remarks. The only hitherto described parasitic isopod from fresh water is *Artystone trysibia* Schioedte 1866 from the body cavity of *Geophagus brasiliensis* in the Humboldt River, Brazil, of which there are six excellent specimens in the British Museum. *Artystone* shows no close affinity to *Badroulboudour* since it can easily be distinguished from it by the following characters: Head: small, retracted, without bosses and lateral horns, eyes well seen in dorsal aspect. No dorsal denticles. Uropods as long as the telson. Antennules of 7–8 articles.

Generic characters. Cephalothorax standing out boldly and not immersed in the collar, with three large rounded bosses anteriorly and three pairs of lateral horns. Eyes concealed by horns in dorsal aspect. The first two free thoracic segments are roughened with denticles dorsally, and elsewhere there are black pigment spots. The antennules are four-articled. The uropods are small, almost completely covered dorsally, three-quarters as long as the telson, exopodite and endopodite inflated, the former curved outwards. Host: probably a fresh-water loricariid.

The type specimen is deposited in the British Museum.

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ACANTHOCEPHALA FROM CHINA

II. TWO NEW SPECIES OF THE GENUS *ACANTHOCEPHALUS* FROM AMPHIBIA[1]

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(With 3 Figures in the Text)

The present report is confined to the species found in Chinese amphibians by Faust in his field studies during the period from 1920 to 1925. Two new species of the genus *Acanthocephalus* are described in this paper and notes on their geographical distribution and host relationships are included along with observations on the occurrence of undetermined species of encysted larval Acanthocephala in amphibian hosts.

The genus *Acanthocephalus* is very widely distributed in fishes and amphibians. Members of this genus are separable with the greatest of difficulty for, as Luehe (1912) has demonstrated, the number of proboscis hooks shows a range of variability unknown in most genera of Acanthocephala. This, combined with the fact that some of the host species of *Rana* and *Bufo* have extremely broad geographical distribution in the continent of Asia, renders recognition of acanthocephalan species unusually difficult.

To the present time there has been no mention in the literature of the occurrence of the genus *Acanthocephalus* in the Chinese fauna. In presenting descriptions of two new species of this genus from Chinese amphibians the writer has reviewed the literature on the occurrence of the genus and its numerous species in Japan and other regions of the Orient. A comprehensive revision of the genus is in course of preparation. In the present paper only those forms apparently near to the new species will be mentioned.

Acanthocephalus sinensis n.sp.

(Figs. 1 and 2)

This species is recognized on the basis of a long series of specimens from which 45 individuals have been selected for critical study. Of these, a female (Van Cleave, No. 2091.11) is designated as holotype. From the remaining series of paratypes a male (No. 2092.9) is designated as allotype. Females 10–15 mm. in length, males 5–8 mm. Proboscis armed with 15–19 longitudinal rows of 4–6 hooks each. Hooks showing very great individual variation with those of

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females tending toward greater size than those of males as is usual in this genus. Hooks on anterior region of proboscis of males ranging from 53 to 94μ, of females 53 to 115μ; on mid-region of males 66 to 103μ, of females 79 to 115μ; on basal region of males 53 to 98μ, of females 53 to 98μ. Embryos 45–60μ long by 12–15μ in diameter.

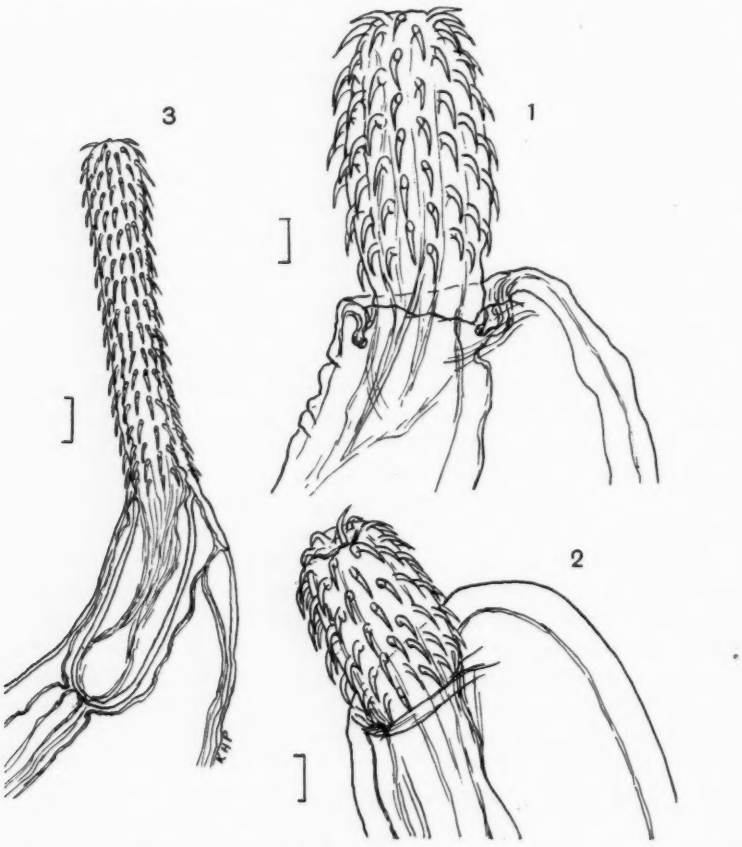

Fig. 1. *Acanthocephalus sinensis*. Proboscis of holotype female. Accompanying each drawing the scale indicating magnification has the value of 0·1 mm.
Fig. 2. *Acanthocephalus sinensis*. Proboscis of allotype male.
Fig. 3. *Acanthocephalus elongatus*. Proboscis of holotype female.

This species may be distinguished from other species of the same genus in the Orient on the basis of size of the embryos in gravid females. The embryos of *Ac. sinensis* are distinctly smaller (45–60 by 13–15μ) than those of the apparently nearest species, *Ac. artatus* (69–83 by 18–24μ). So far *Ac. artatus* has been reported from Japan only. Other representatives of the genus de-

scribed from amphibians of the Orient (*Ac. lucidus*, *Ac. nanus* and *Ac. bufonis*) all have embryos clearly larger than those of *Ac. sinensis*. The embryos of *Ac. acerbus* and of *Ac. aculeatus*, recorded from Japanese fishes, fall within the size range characteristic of *Ac. sinensis*, but the number of longitudinal rows of proboscis hooks in *Ac. sinensis* is constantly greater than for either of the above-mentioned species.

Hosts. *Rana nigromaculata* and *Bufo formosus*, in intestine.

Type locality. Changsha, Hunan province (central China). Additional localities: Shaohsing, Chikiang province (east central China), and Wuchang in Hupek province (central China).

Acanthocephalus elongatus n.sp.

(Fig. 3)

The recognition of this species is based on a single immature female which becomes holotype (Van Cleave, No. 2092.5).

Holotype female 4·1 mm. long with a cylindrical proboscis 0·86 mm. long and 0·38 mm. in diameter. Proboscis hooks in 16 longitudinal rows of 13–15 hooks each. Hooks on anterior region 33–45μ long, on middle of proboscis about 57μ and near base about 45μ.

Type host. *Bufo formosus*, in intestine.

Type locality. Changsha, Hunan province, China.

Ac. elongatus was found associated with *Ac. sinensis* in the same host individual.

The very slender, much elongated proboscis clearly distinguishes this species from all other members of the same genus. The European species *Ac. anthuris* closely approaches *Ac. elongatus* in hook number but the hooks of the latter are much smaller than those of *Ac. anthuris*. The proboscis of *Ac. elongatus* is much larger than that of *Ac. anthuris*. *Ac. gotoi* from Japanese fishes also has hook numbers comparable to *Ac. elongatus* but the proboscis of the latter is considerably larger and much more filiform.

Representatives of the genus *Acanthocephalus* as here recorded are not general in their distribution. In fact the geographical distribution of the parasites is not coincident with the distribution of the suitable hosts. In north China, the province of Chihli, in which Peiping is located, and Shanshi which joins it on the west have amphibians which are wholly free from members of the genus *Acanthocephalus*. Faust's collections from amphibians from these northern provinces are limited to post larval worms encysted in mesenteries and other viscera. All of these cysts, so far as they were capable of determination, contained immature worms of the genus *Centrorhynchus*, adults of which doubtless occur in birds. The genus *Acanthocephalus* is well represented in amphibians of the central provinces Hupek and Changsha and the coastal province Chikiang. Here also the cysts of post larval *Centrorhynchus* are of common occurrence.

Water snakes (particularly *Natrix tigrina*) which feed upon amphibians very commonly carry *Acanthocephalus sinensis* in the intestine. Similar accidental presence of acanthocephalans in the intestine of predatory animals has been encountered in other regions of the earth. Some of the members of the genus *Acanthocephalus* were taken by Faust from *Agkistrodon blomhoffii* of Changsha province. These are in poor state of preservation and though the proboscides are either missing or introverted the females bear embryos considerably larger than those of *Acanthocephalus sinensis*. These embryos (66–72 by 15–18μ) may belong either to an undescribed species or to *Ac. elongatus*.

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ON A NEW CASE OF PARASITISM OF SNAIL (*VERTIGO GENESII* GREDL.) BY A DIPTEROUS LARVA

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From the Molteno Institute of Biology and Parasitology, University of Cambridge

(With 13 Figures in the Text)

Introduction

The object of this paper is the description of a dipterous larva based on the study of six specimens of larvae obtained by Mr R. A. Phillips from living specimens of the snail *Vertigo genesii* Gredler which he had caught at Cloanascragh Bog, near Taum, Co. Galway. Three larvae were received in October 1933 through Prof. Boycott, and three in September 1936 directly from Mr Phillips. In a letter accompanying the specimens Prof. Boycott makes the following remark: "Considering that the whole snail shell is only about 2 mm. × 1 mm. the larvae seem very big." In fact some of the shells are distinctly smaller than the adult larvae, which when mounted are 2·0–5·0 mm. long, and 0·3–1·5 mm. in diameter.

Host

Vertigo genesii Gredler is a small snail, the shell of which (Fig. 1) measures about 1·8–2·0 × 1·0–1·1 mm. It was discovered in Ireland, first in a fossil state by A. W. Stelfox in 1922 and later as a living species by R. A. Phillips in 1924.

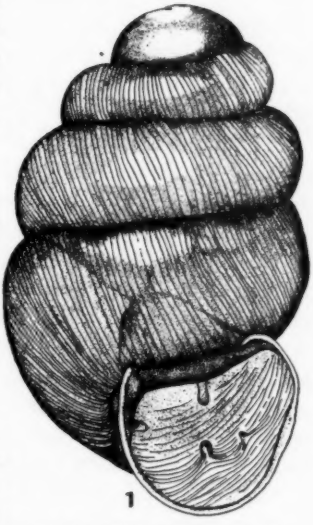

Fig. 1. Shell of *Vertigo genesii*, ×42.

Observations on the living larva

Of the three living larvae received directly from Mr Phillips at the beginning of September 1936, two died within a fortnight. The third lived normally up to 2 November. It was kept in moist grass and a little mud, and fed only on pieces of freshly killed snails washed free of mucilage. It showed marked repulsion to decomposing snail tissue, or to snails dead more than 5 hours.

Generally the larva begins to feed from the edge of the mantle. The pharyngeal mass moves forwards, the teeth of the ventral pair of sclerites

and of the lateral hooks close upon the snail tissue, and the pharyngeal mass moving backwards, a piece of the tissue is torn off and taken up into the mouth. The process is repeated rhythmically. During this process the head of the larva is attached to the snail tissue by means of integumental hooks. In this way the parasite penetrates the snail until its whole body is buried except the posterior spiracles. The snails used were small garden varieties, such as young *Helix aspersa*, *Trichia striata*, and *Retinella nitidula*. From time to time the larva has a curious habit of erecting its head and swallowing air, which may be seen passing down the alimentary canal. This occurs even during feeding.

Morphology

The larva is elongated, narrow at the anterior end, and broadest at the sixth abdominal segment. The segmentation of the larva is partly masked by secondary transverse folds, but the separate pseudocephalon, the three thoracic and eight abdominal segments may be recognized with care. The pseudocephalon, as in other cyclorrhaphous larvae, is divided by means of a longitudinal groove into two lateral lobes. When the larva extends itself the thoracic can be distinguished from the abdominal segments by the outline of the former being more or less straight and the folds obliterated, while in the abdominal segments the folds and protuberances persist. The division between the seventh and eighth segment is well marked by a complete dorsal transverse fold. Four lobes form the posterior portion of the last (eighth) segment (Figs. 3 and 6).

The cuticle is colourless and transparent, and most of the internal structures can be seen through it. Except for the greater part of the pseudocephalon and the two pad-like areas lateral to the anus, the whole body is covered by minute scales, which gradually become spinous towards the posterior end of the larva. On the ventral surface of the pseudocephalon, behind the mouth, there is an area bearing prominent brown hooks with long bases, among which six semicircular rows can be defined (Fig. 5*h*). The anus (Fig. 13) is situated on the ventral surface of the eighth abdominal segment. It is oval and surrounded by chitinous folds, lateral to which are two pad-like areas. There are a large number of dark hooks anterior to the anal region, and a few smaller ones posterior to it. The anterior hooks have broad bases, and some of them have two processes.

On the ventral surface of each abdominal segment the cuticle has sensory papillae, which are absent from the thoracic segments (Figs. 3 and 9). Each papilla consists of a ring of smaller scales surrounded by a ring of larger scales, in the centre of which is a small conical sensillum. Through the skin of the living larva (mounted between slide and cover-slip) a nerve can be seen, near each of these structures, coming from the direction of the central nervous system. It forms a large ganglion near the papilla and sends a small but distinct nerve to the central sensillum (Fig. 13). These papillae are arranged

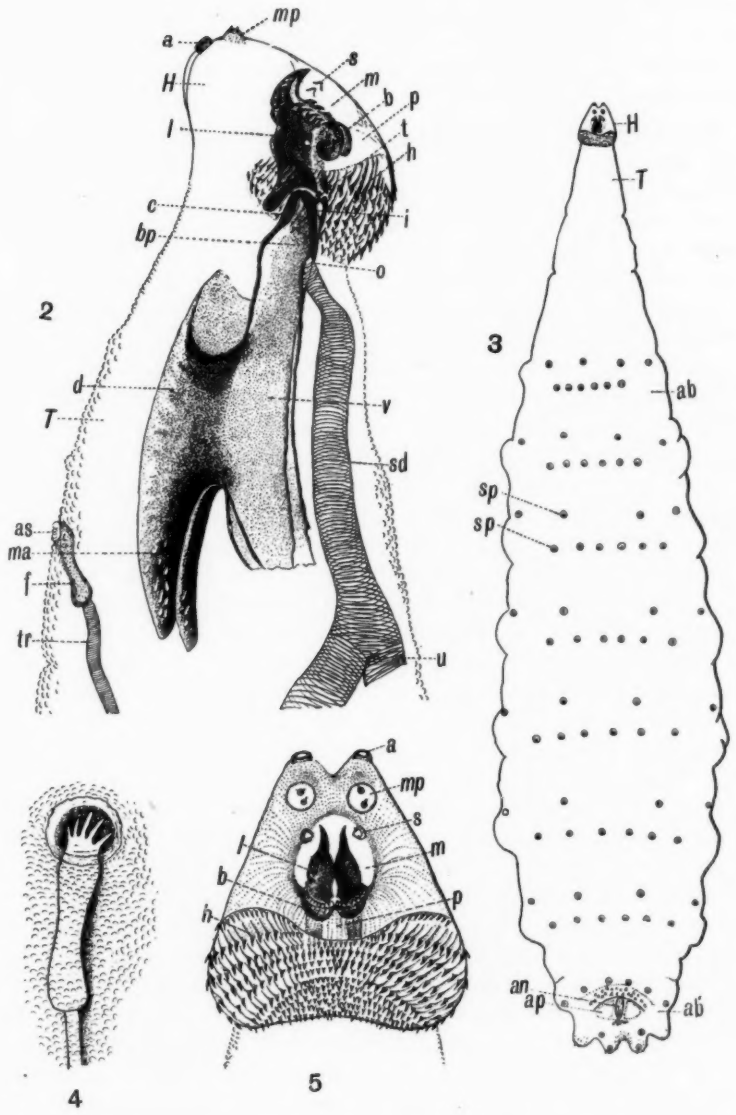

Fig. 2. Cephalopharyngeal armature of larva seen from the right side, ×221.
Fig. 3. Ventral view of fully extended larva, showing arrangement of sensory papillae, ×28.
Fig. 4. Prothoracic spiracle, with five finger-like papillae as seen in the living larva, ×625.
Fig. 5. Ventral view of pseudocephalon, showing mouth-parts, ×202.

in transverse rows of six in each segment. Anterior to them there is another row of four widely separated papillae, except in the last segment in which the row of four papillae is posterior. The dorsal surface of each body segment shows a tranverse row of very fine spines, which are most clearly seen on the thoracic segments.

Mouth-parts. The pseudocephalon is pear-shaped when extended, and each of its lobes bears on the anterior margin a pair of rudimentary antennae, terminated by a circular surface, which is bounded by a rim. Behind these, on the ventral side, is a pair of sessile maxillary palps, each having two sensory hairs on its surface. On the anterior side of the mouth there is a pair of minute buccal sense organs. The anterior part of lateral hooks and the toothed margin of saucer-like sclerites described below can be seen; the former projecting from the middle and the latter from the posterior boundary of the mouth (Fig. 5).

The *cephalopharyngeal armature* (Fig. 2), like that of other cyclorrhaphous dipterous larvae, is composed of (1) two lateral hooks, (2) an intermediate or hypopharyngeal sclerite, (3) the basal or pharyngeal portion, and (4) a ventral pair of saucer-like sclerites, homologous with the "arc median ventral" of the Anthomyid carnivorous larvae described previously by Keilin (1917 *a*). Each of the lateral hooks is strongly chitinized and almost uniformly black. It is curved ventrally, and shows four distinct and backwardly directed teeth, on its concave side. In two specimens the hooks of one side had four teeth and of the other five. The truncated part has a circular hole laterally towards the ventral side. The intermediate sclerite is not a separate structure, as it is usually in the third stage larvae, but is completely fused with the basal or pharyngeal portion as is the case in some other parasitic larvae such as *Neottiophilum praeustum* (Keilin, 1924) or *Melanophora roralis* L. (Thompson, 1934). Among saprophagous larvae this condition is found in *Leptohylemyia coarctata* Fall. (fig. by Keilin, 1917*b*) and in three Acalyptrate larvae, viz. *Chloroptoeniopus* Meig., the gout-fly of barley, *Meromyza nigriventris* Mcq. and partial fusion in *Balioptera combinata* L. described by Frew (1923). On each side of the anterior end of the hypopharyngeal sclerite, in combination with the clubbed part of a marginal thickening, arising from the basal sclerite, forms an articulating rounded surface at the base of the lateral hooks. There is a minute transverse sclerite which seems to be made up of a pair of cross-bars with knobs at their free ends, between the anterior ends of the hypopharyngeal sclerite. On the ventral surface a thick chitinous membrane unites the greater part of the hypopharyngeal sclerites of the two sides, and the basal plates. In this membrane the opening of the common salivary duct is found. The membrane ends a little behind this perforation, so that the rest of the basal plates of the two sides are separated along the medio-ventral line.

The basal or pharyngeal sclerite is composed of two strongly chitinized plates on each side, with posterior emarginations, and has a structure very similar to that of other cyclorrhaphous Diptera.

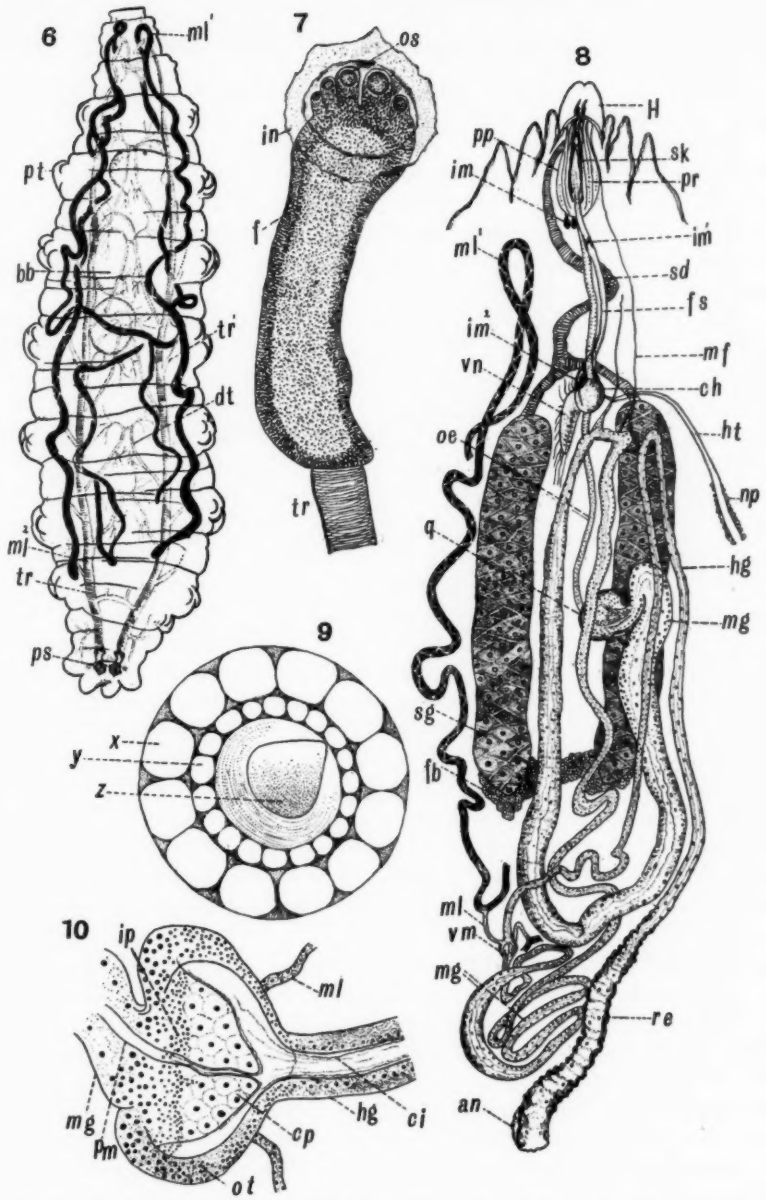

Fig. 6. Drawing of living larva in a state of rest with pseudocephalon and prothorax retracted, ×29.

Fig. 7. Prothoracic spiracle from a fixed preparation showing five spiracular papillae with openings, ×1579.

Fig. 8. Alimentary system, from dissection of larva stained with haemalum. Membranous frontal sac (*fs*) and cerebral hemispheres (*ch*) are displaced to the right to show the course of oesophagus, ×35.

Fig. 9. Ventral abdominal sensory papilla, ×2115.

Fig. 10. Valve at the posterior end of mid-gut, ×208.

The pharynx is smooth and completely devoid of the projecting longitudinal ridges found in saprophagous dipterous larvae.

The ventral pair of saucer-like buccal sclerites are quite separate from the lateral hooks arising from the inner surface of the labial part of the mouth. On their anterior margin, facing the teeth of the lateral hooks, they bear strong teeth, curved inwardly and acting as a pair of powerful lower jaws. These buccal sclerites can be homologized with the "arc median ventral" of carnivorous anthomyid larvae.

Alimentary canal. The pharyngeal skeleton is surrounded dorso-laterally by protractor muscles which run from the posterior ends of the wings of the basal plates and are fixed anteriorly to the chitinous ring between the pseudocephalon and the first thoracic segment. The pharyngeal pump (Fig. 8) is pear-shaped and is joined at its base by the oesophagus. The latter, after passing between the cerebral hemispheres and the ventral ganglionic nerve mass, reaches nearly the middle of the body and opens into a thick walled proventriculus.

The mid-gut is the longest part of the alimentary canal. No gastric caecae are present, and the peritrophic membrane can be seen throughout the whole length of the mid-gut. The first part of the mid-gut is wide. The narrower part of the mid-gut which follows it (Fig. 8) forms close convolutions towards the posterior end but becomes wider again for a short distance on the left side. The part into which the malpighian tubules open is thick-walled, rounded, and has an inner valve (Fig. 10). It is composed of large round cells with prominent nuclei, and is continuous with the layer of epithelial cells of the mid-gut. The peritrophic membrane is continued into the valve.

The hind-gut commences at the valve. It is narrow, and first travels forwards beyond the proventriculus and then backwards, gradually becoming wide. A tough chitinous tube can be clearly seen within throughout the length of the hind-gut. If a part of the hind-gut is pulled the epithelial and muscular layers tear off, leaving the internal shining chitinous tube intact. This tube is probably the continuation of the chitinous intima of the rectum.

Salivary glands. The salivary glands are the most conspicuous structures in the body of the larva. They are sac-like and consist of a uniform layer of large quadrangular cells, with large rounded nuclei and clear cytoplasm. The salivary ducts join together beneath the oesophagus, a little in front of the brain. The anterior common duct thus formed runs forwards and opens into the ventral portion of the hypopharyngeal skeleton.

Malpighian tubes. A pair of malpighian tubes open into the side of the valve-bearing region of the mid-gut, so that the excretions discharged by the former can only flow into the hind-gut. Each tube is short, narrow, unpigmented and divides into a pair of very long thick convoluted dark brown tubules. All four tubules terminate near the posterior end of the body.

Tracheal system. The larva is amphipneustic. The anterior spiracles (Fig. 2 *as* and Figs. 4, 7) lie on each side of the prothoracic segment, in a pit

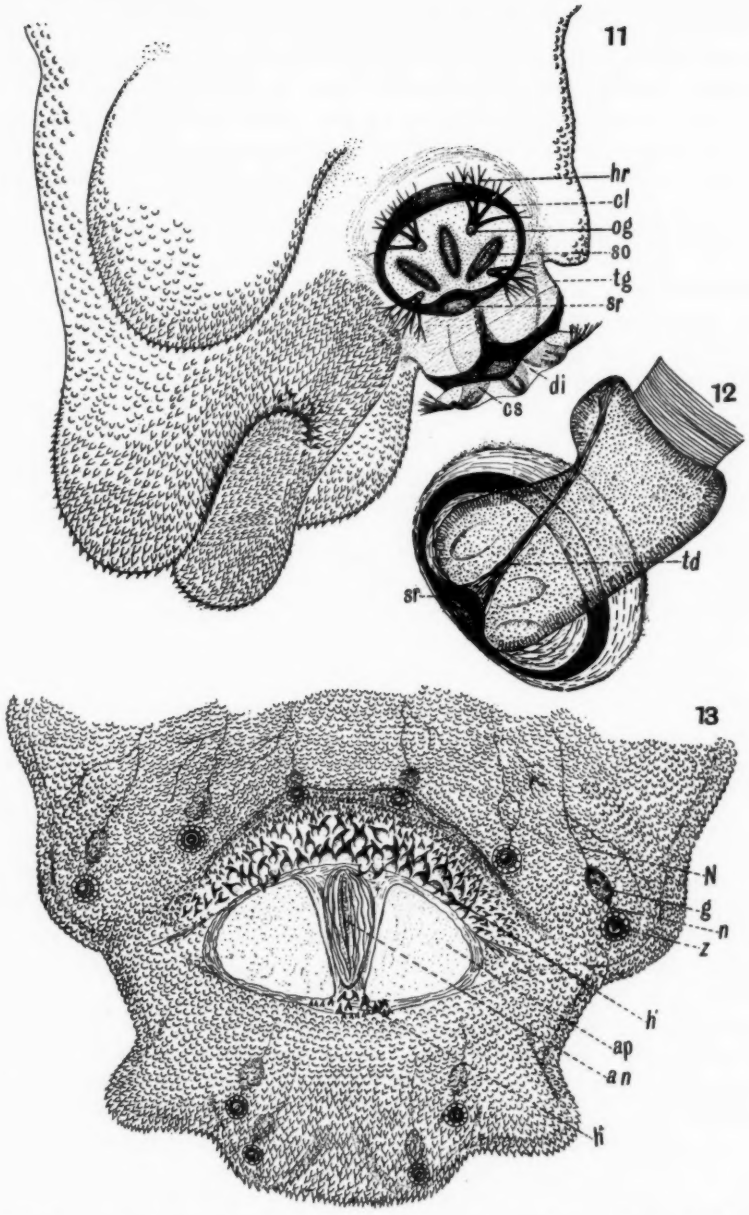

Fig. 11. Lateral view of the eighth abdominal segment giving facial view of one spiracle and lateral view of the other, × 360.

Fig. 12. Posterior spiracle and its felt chamber seen from the ventral surface of the eighth abdominal segment by transparency, × 537.

Fig. 13. Ventral surface of the eighth abdominal segment, × 203.

formed by the contraction of the surrounding cuticle. Each spiracle has five papillae. The posterior spiracles (Figs. 6 *ps*, 11, 12) are placed on a pair of prominences on the dorsal surface of the eighth segment, surmounted by umbrella-like discs, bearing three converging oval spiracular openings. Beneath each spiracular opening is a small chamber which communicates with the atrium or felt chamber. Between the disc and the prominence, on which it is situated, is a strongly chitinized dark collar-like ring, in which the scar of the previous instar is found. On the disc four sets of well-developed branched hairs are present arising from the outer margin of the openings of the perispiracular glands. The spiracular openings are bounded by distinct lip-like margins, and show minute trabeculae such as line the felt chambers of the anterior and posterior spiracles.

The distribution of the rest of the tracheal system is essentially similar to that of other cyclorrhaphous larvae (Fig. 6).

Identity of the larva

The general appearance of the cephalopharyngeal armature, the amphipneustic respiratory system and the presence of the three spiracular openings, together with the large external scar on the posterior spiracles, show that the larvae have already reached the third stage.

The absence of the ventral pharyngeal ridges is an important character, which indicates that the larvae are biontophagous, i.e. feeding on living organisms (Keilin, 1915), confirmed further by the fact that in the laboratory the larvae ate only living tissue of snails. On the other hand, the structure of the head and of the mouth-parts excludes the possibility of a carnivorous or phytophagous mode of life (Keilin, 1915). The larvae are undoubtedly parasitic. So far our knowledge concerning the life history and morphology of dipterous larvae parasitic in snails is confined to one case, that of *Melinda cognata* Meig. in *Helicella* (*Heliomanes*) *virgata* De Costa (see Keilin, 1919). The larvae of *Melinda cognata*, however, reach a much larger size, even in their second stage, and the cephalopharyngeal armature of their third stage differs markedly from that of the larva described above.

It may be mentioned here that in 1843 Goureau had bred a few specimens of *Melanophora helicivora* Goureau from comparatively small snails, *Helix conspurcata*. The observation, however, has never been confirmed by other workers. The larvae of *Melonophora roralis* L. have been found parasitic on wood-lice, and their life history and morphology were recently described by W. R. Thompson (1934). The general structure of these larvae, and especially their cephalopharyngeal armature, is very different from those of the larva described above.

We can see therefore that the larvae obtained from *Vertigo genesii* are the third stage larvae of a parasitic cyclorrhaphous fly. Morphologically they differ markedly from those of *Melinda cognata*, *Melanophora roralis* or

any other species so far described. This forms a new case of a dipterous larva parasitic on a mollusc, and considering the very small size of the host, the larvae must belong to a very small fly of the family of Sarcophagidae, or Tachinidae (including Dixiidae). The further possibility of its belonging to a small *Acalyptrate* fly also cannot be excluded.

Lettering of Figures

a antenna.
ab first abdominal segment.
ab' eighth abdominal segment.
an anus.
ap anal pad.
as anterior spiracle.
b pair of ventral buccal toothed sclerites.
bb air bubble in alimentary canal.
bp part of the basal plate fused with hypopharyngeal sclerite.
c clubbed part of the marginal thickening of basal plate.
ch cerebral hemispheres.
ci chitinous intima.
cl collar-like chitinous ring.
cp conical plug.
cs chamber below spiracular opening communicating with felt chamber.
d dorsal wings of the basal plate.
di spiracular disc.
dt dorsal tracheal commissure.
f felt chamber.
fb portion of fat body.
fs membranous frontal sac.
g nerve ganglion.
H pseudocephalon.
h, h^1, h^2 hooks with long, broad and short bases respectively.
hg hind-gut.
hr branching chitinous hairs.
ht heart.
i intermediate or hypopharyngeal sclerite.
im, im^1, im^2 imaginal buds of labium, pharynx and compound eyes respectively.
in external margin of integumental pit.
ip basal part of the valve containing imaginal tissue.
l lateral hook bearing four teeth.
m mouth.
ma points of muscle attachments.
mf muscle fibre arising from the mid-gut.
mg mid-gut.
ml, ml^1, ml^2 proximal unpigmented, anterior loop and terminal parts of malpighian tubules.
mp maxillary palp.
N nerve.
n nerve between ganglion (*g*) and sensory papilla.
np pericardial nephrocytes.
o opening of the common salivary duct.
oe oesophagus.
og opening of perispiracular glands.
os opening of spiracular papilla.
ot outer wall of the valve containing imaginal tissue.
p region of labial palp.
pm peritrophic membrane.
pp pharyngeal pump.
pr protractor muscles.
ps posterior spiracle.
pt lateral protuberance of abdominal segment.
q proventriculus.
re rectum.
s buccal sense organs.
sd common salivary duct with spiral of chitinous intima within.
sg salivary gland.
sk pharyngeal skeleton.
so spiracular opening.
sp sensory papillae.
sr spiracular scar.
T prothoracic segment.
t transverse sclerite between anterior ends of hypopharyngeal sclerites.
td strands from the inner surface of the scar to the base of felt chamber.
tg integumental prominence.
tr, tr^1 tracheal trunk and a lateral branch.
u union of salivary ducts.
v ventral wing of basal plate.
vm valve at the end of the mid-gut.
vn ventral nerve mass.
x scale of outer ring.
y scale of inner ring.
z sensillum.

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CYSTICERCOSIS IN DEER

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A case of a heavy infestation of *Cysticercus tenuicollis*, terminating fatally in a deer, was recently afforded by one of the experimental animals of the Dominion Entomological Branch (Livestock Insect Investigation Laboratory) at Kamloops, B.C.

The host, a 2-year-old mule deer (*Odocoileus hemionus*), was obtained as a yearling from a farmer at Savona, B.C., on 7 October 1935. During the following 10 months it was in the possession of the Branch field laboratory where through the fall and winter of 1935 it had been subjected to several infestations of the moose and cattle tick, *Dermacentor albipictus* Packard.

Throughout the summer of 1936 the deer exhibited a general emaciated and weakened condition, with dryness and loosening of hair. Its state was attributed to the previous tick infestations, since it is a well-known fact that stock may be severely weakened by heavy attacks from these parasites.

On 17 August 1936 the deer died. Examination, on necropsy, revealed the liver and mesenteries to be distended with hundreds of cysts. Occasional cysts were also distributed in the lungs. The parasites were identified through the kindness of Dr W. E. Swales of the Institute of Parasitology, Macdonald College, as *Cysticercus tenuicollis*. The mature form of this cestode parasitizes the dog, wolf, coyote and related carnivores.

It is of interest here to note that Fenstermacher & Jellison (1933) observed the same species of cyst in the livers of eight of thirteen sick moose that they examined in 1931 and 1932.

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A NOTE ON *CAPILLARIA AËROPHILA* (NEMATODA)

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(With 1 Figure in the Text)

In a previous paper (1931) the writer described the presence of a spicule in the male of *Capillaria* [*Hepaticola*] *hepatica*, and gave reasons for believing that the apparent presence or absence of a spicule in the males of forms closely related to it is not a reliable taxonomic character. It was suggested that the genus *Eucoleus* Dujardin, which, like *Hepaticola* Hall, was based mainly on the supposed absence of a spicule, should likewise be suppressed as a synonym of *Capillaria*. Teixeira de Freitas & Lent (1935, 1936), in accepting this view, have drawn attention to an observation recorded by Creplin (1849), which had been generally overlooked, to the effect that a spicule is present in the genotype of *Eucoleus* (*Trichosomum aërophilum* Crepl., in Ersch & Gruber, 1839). Up to the present Creplin's observation has not, so far as the writer is aware, been confirmed[1]. Some specimens of *Capillaria aërophila* from the lungs of silver foxes were recently received from Mr C. V. Watkins, M.R.C.V.S., who had noticed in a living male specimen what appeared to be a spicule projecting from the everted spicule-sheath, and enclosed a sketch of it in his letter. On examining the preserved material, the writer was able to confirm this interesting observation. In the specimen referred to by Mr Watkins, and in another individual, a very delicate structure, apparently a spicule, was seen projecting for a short distance beyond the end of the partly everted sheath. In a third specimen (see Fig. 1) this structure protruded to the extent of about 0·55 mm. from the sheath, which in this case was completely everted. It seems impossible to interpret this very slender structure otherwise than as a spicule. It is extremely flexible and hardly, if at all, chitinized, and has an exceedingly thin, transparent, colourless, tubular wall enclosing a lumen which appears to contain a few granules. The thickness of the protruding portion, for the greater part of its length, does not exceed 3μ. It increases to about 4μ proximally, near the point of emergence from the sheath, while just before the distal end there is a slight fusiform expansion reaching a maximum diameter of about 5μ.

The portion of the spicule remaining within the sheath is extremely difficult to detect, probably because of its lack of chitinization and of the refringent properties of the spines covering the sheath. The total length of the spicule, therefore, is unknown. In specimens in which the sheath itself is introverted, no trace of the spicule has been seen at all.

[1] Since sending this note to press, the writer has seen a paper by O. Wagner (*Senckenbergiana*, Frankfurt, XVIII, p. 245 (31 Dec. 1936)) in which the presence of a spicule in *C. aërophila* (from the cat) is described and illustrated by photographs.

The sheath is completely covered with spines. When fully everted, as in the specimen figured, it shows a somewhat bell-shaped distal expansion on which the spines are much shorter than those on the rest of the sheath. When the sheath is introverted this distal portion becomes, of course, its anterior end, and the spines, which now form the lining of the sheath, point towards the posterior extremity of the body.

This two-fold confirmation of Creplin's statement as to the presence of a spicule in the genotype of *Eucoleus* renders it no longer possible to maintain the distinctness of this genus, which must be regarded definitely as a synonym of *Capillaria*, the correct name of the genotype being *C. aërophila* (Creplin, 1839) Railliet, 1915.

Several observers have described the eggs of *C. aërophila*. Their extreme measurements, as given in different descriptions, are as follows:

Length (including polar plugs) 0·059–0·08 mm.

Length (excluding polar plugs) 0·055–0·068 mm.

Width 0·0288–0·04 mm.

To these figures the writer has nothing to add, the measurements of the eggs seen (with the exception of an occasional "giant" egg) falling between the extremes. One point, however, may be mentioned to which attention has not, perhaps, been sufficiently directed. This concerns the surface-pattern of the egg-shell. Dujardin (1845) describes the shells as "granular". Christenson (1935), who has given the most detailed account of the eggs of this species, also says "leur coque est finement granuleuse", and the same statement has been made by other comparatively recent authors (most of whom were probably quoting Dujardin). Riley & Christenson (1931) are more correct when they speak of "thick, netted shells". Good figures of the eggs are given by Nöller & Schmid (1932), showing a network-like pattern which the writer finds to be a constant feature of the species. In this respect the eggs very

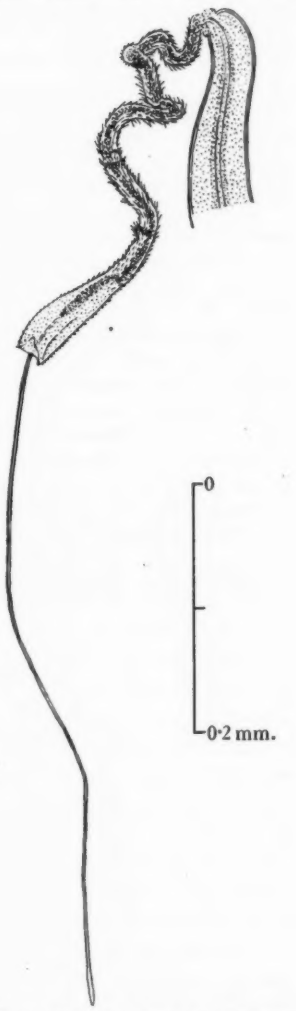

Fig. 1. *Capillaria aërophila*. Posterior end of male; lateral view, showing the terminal portion of the body, the everted spicule sheath and the spicule.

closely resemble those of *C. gastrica* (see Baylis, 1926, Fig. 2 A). The network appears to be composed of structures within the thickness of the outer layer of the shell.

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THE METHOD OF DIVISION OF *TREPOMONAS AGILIS* IN CULTURE

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(With 9 Figures in the Text)

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I. Introduction

Trepomonas agilis, first described by Dujardin (1841), is commonly found in ponds rich in decaying organic matter, and in infusions. This flagellate was well known to early workers (Stein, 1878; Kent, 1880–2; Bütschli, 1878, 1889; Klebs, 1892; and others), but owing to its rapid movements they had difficulty in studying its structure and counting its flagella. More recently Wenyon & Broughton-Alcock (1924) found a *Trepomonas* occurring, together with a species of *Bodo*, coprozoically in a mucous stool from a human being suffering from colitis.

In addition to its free-living and coprozoic habitats, *Trepomonas* has been described from the intestines of a variety of hosts. Thus Alexeieff (1909) found *T. agilis* when examining the intestinal fauna of several species of Amphibia, and later (1910) he found a member of the genus in the rectum of *Box salpa*. Recently Lavier (1935) has found *Trepomonas* in the intestine of the common *Triton*, and in the tadpoles of *Rana temporaria*, *R. esculenta*, and *Alytes obstetricans*; and Das Gupta (1935) has described this flagellate from the caecum of *Terrapene major*, *Kinosternon hippocrepis*, and *Chelydra serpentina*.

To Dangeard (1902) we owe the first precise description of the nucleus of *Trepomonas*. He stated that the two nuclei formed an arc at the anterior end of the body. Later (1910) he gave a more detailed description of *T. agilis*. He observed the division of the nuclei, noting that each formed a spindle and that the daughter flagellates each possessed two nuclei of different origin. His figures (Pl. 25, figs. 21 and 22) of the dividing flagellates show no details of nuclear structure and no flagella. Lavier (1936) has described the torsion of the body of *Trepomonas* and mentions that nuclear division is simultaneous in the two nuclei and that spindles are formed; but he gives no figures and his description adds little to that of Dangeard.

On 25. v. 36 I obtained a supply of *Trepomonas agilis* from a pond at Shelford, near Cambridge. Extremely rich cultures of this flagellate, together with a mixed crop of bacteria, were obtained in a medium consisting of an inspissated horse serum slope covered with inactivated horse serum (1 : 10) in distilled water. The cultures needed to be transplanted every 4–7 days. They grew at room temperature (i.e. 18–20° C.). The strain is still (16. xi. 36) growing well. Cultures were also obtained in hay infusion, but the growth was never very rich. Flagellates in all stages of division were numerous in the serum cultures, and as no detailed description of division existed I decided to study it.

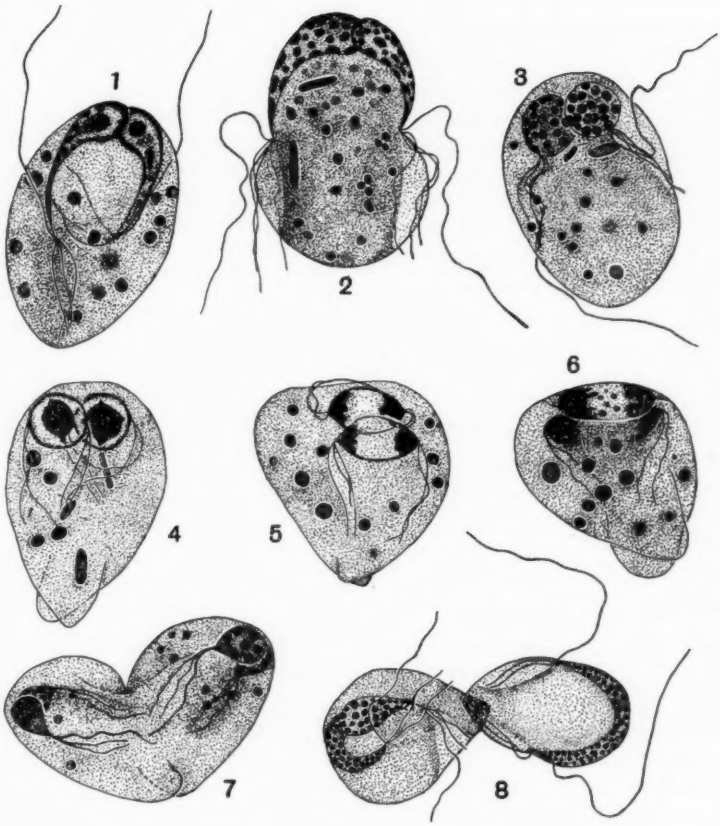
The best preparations of the flagellates were obtained by fixation with Schaudinn's solution containing 5 per cent glacial acetic acid; but good preparations were also obtained with Bouin's fluid. Heidenhain's iron haematoxylin, counter-stained with eosin, proved to be the most useful staining method; but Feulgen's nucleal reaction, as described by Robertson (1927), was also used. In the study of the flagella Noland's (1928) "fixative-stain combination" was of great assistance.

II. Morphology and method of division

Trepomonas agilis, when grown in serum or hay infusion, measures 10–14 × 6–8μ. As first shown by Klebs (1892) there are eight flagella arising in two groups of four, one group on either side of the body. The two points of insertion of the flagella lie on opposite sides of the body about half-way between the anterior and posterior ends. One flagellum of each group is long and thick and projects outwards, the other three are short, and lie in deep grooves of which there is one on either side of the body. The two groups of three short flagella do not project outside the depressions. Whereas the long flagella appear to propel the flagellate, each group of short flagella, by its flickering movements, keeps a stream of water constantly flowing through the depression in which it lies.

Although in the cytoplasm there are many food vacuoles, usually containing bacteria, I have been unable to discover a mouth or to see the food being ingested. Dangeard (1910), however, describes two mouths, one in each groove at a point near to the insertion of the flagella. The cytoplasm circulates actively inside the body, as was noticed by early workers. Several clear vacuoles of varying sizes can be seen moving with the cytoplasmic current. The smaller ones gradually become bigger. Their maximum size appears to be fairly constant, although it has not been possible to measure them owing to the rapidity with which the flagellate swims. When a vacuole which has attained its full size reaches the posterior end of the body it contracts and disappears. These vacuoles therefore appear to be true contractile vacuoles.

There are two nuclei, as Dangeard (1902, 1910) has shown. Together they form a horseshoe-shaped structure bordering the anterior end of the body (Figs. 1 and 9). Each nucleus forms one-half of the horseshoe, and their posterior ends are the points from which the two groups of four flagella take their



Figs. 1–8. The figures were drawn with an Abbé camera lucida with a 1/12 in. fluorite oil-immersion lens at an approximate magnification of 2640 diameters. The flagellates were fixed with Schaudinn's or Bouin's fluid and stained with iron haematoxylin.

Fig. 1. *Trepomonas agilis* with nuclei at resting stage.
Fig. 2. Nuclei becoming granular prior to division.
Fig. 3. Nuclei becoming spherical.
Fig. 4. Chromatin masses in centre of nuclei. Each group of four flagella divided into two groups of two.
Fig. 5. Both nuclei have formed spindles.
Fig. 6. Spindles elongating and becoming absorbed at the centre.
Fig. 7. Cytoplasmic fission in progress.
Fig. 8. Two daughter flagellates separating.

origin. When the resting nucleus is stained with haematoxylin a deposit of siderophilic material is seen on the inside of the nuclear membrane. In some individuals this layer is formed of discrete granules. With Feulgen's reagent it stains red (Fig. 9), and is therefore chromatin. Inside this chromatic layer, in each nucleus, is a clear area containing one large granule or sometimes two. These also proved, with Feulgen's reagent, to be chromatin. Wenyon (1926) has suggested that these granules are the true nuclei, and that they divide before the division of the "horseshoe structure" (the two closely applied nuclei). Observations upon dividing individuals, however (see below), refute this suggestion.

The members of each group of four flagella arise close together from the posterior end of the corresponding nucleus. It has been impossible, in any preparations, to detect basal granules. The two groups of flagella always appear to arise directly from the posterior tips of the nuclei.

Fig. 9. *Trepomonas agilis* fixed with Schaudinn's fluid and subjected to Feulgen's nucleal reaction.

Stein (1878) saw and figured individuals which he concluded were either dividing longitudinally or undergoing copulation. Bütschli (1878) also saw individuals which suggested to him longitudinal division; but Klebs (1892) apparently watched the whole process though he could not make out the details.

Dangeard (1902, 1910) showed that the two nuclei divide simultaneously, by spindle formation, but he gave no details of the arrangement of the chromatin nor did he describe what happens to the flagella or the two grooves.

When division is taking place the flagellate ceases to progress though it rotates frequently. The body gradually grows broader at the anterior end. Both groups of four flagella can be seen to move apart in two groups of two. Cleavage of the body begins at the anterior end and continues towards the posterior. The two daughter flagellates pull in opposite directions, so that just before cleavage is complete the superficial appearance of the dividing organism suggests transverse division (Fig. 8).

In the earliest stages of division, before the body of the flagellate has undergone the changes described above, the nucleus becomes filled with large granules (Fig. 2) which when tested with Feulgen's nucleal reaction prove to

be chromatin. Each nucleus (Fig. 3) then becomes spherical and is filled with discrete granules of chromatin. The points of attachment of the flagella are still on the nuclear membrane but no basal granules are visible. Later (Fig. 4), the greater part of the chromatin condenses into a central, irregularly shaped mass, but the nuclear membrane is still siderophilic. Feulgen's reaction, however, shows that whereas the central mass is chromatin the deposit on the membrane is not. It is at the time when the nuclei have just become spherical that each set of four flagella divides into two pairs. The pairs take up their positions at the opposite poles of the nuclei (Fig. 4), but no basal granules are visible, and no centrodesmose connects the pairs. The nuclei become spindle-shaped (Fig. 5), a pair of flagella being attached to either pole of each spindle. The central mass of chromatin divides without the formation of any chromosomes. A compact mass of chromatin forms at each pole. As the body of the flagellate broadens the spindles elongate and eventually their central parts (Fig. 6) appear to be absorbed. There is no evidence that the nuclear membrane constricts round the middle of the spindle. A complete membrane is later formed around each daughter nucleus (Fig. 7). The daughter nuclei contain large chromatin granules, and just before cleavage of the body takes place they become very numerous (Fig. 8). After separation of the daughter flagellates the granular appearance gradually changes to that of the normal resting nucleus (Fig. 1). At the time when cleavage of the body begins (Fig. 7) a third flagellum grows from the point on the nuclear membrane from which the two original flagella arise, though occasionally (Fig. 5) a new flagellum may appear at an earlier stage. The fourth flagellum arises after the separation of the daughter flagellates. During division the difference in length and thickness of the flagella is not so noticeable as in the non-dividing flagellate.

III. DISCUSSION

In the possession of two nuclei and two sets of flagella *Trepomonas* resembles *Hexamita*. Both genera include free-living and parasitic forms. I had occasion some years ago (Bishop, 1933) to study division in *Hexamita gigas*, a flagellate occurring in the alimentary canal of the horse-leech (*Haemopis sanguisuga* = *Aulastomum gulo*). In this species basal granules are visible in both the dividing and the undividing flagellates. In *Trepomonas agilis*, using the same technique as that employed in my study of *Hexamita gigas*, I have failed to demonstrate basal granules at any stage. It is to be concluded that in this flagellate either the basal granules are extremely small and closely applied to the nuclear membrane and thus impossible to demonstrate or that the flagella arise directly from the nuclear membrane. In both genera the nuclei divide simultaneously by spindle formation. In *Hexamita gigas* (Bishop, 1933, figs. 6–13) an achromatic thread persists between each pair of daughter nuclei until cytoplasmic division occurs. Such an achromatic structure does not occur in the dividing nucleus of *Trepomonas agilis*. In neither genus were definite

chromosomes formed. Neither in cultures of *T. agilis* nor of *Hexamita gigas* was encystment or copulation seen.

I should like to thank Mr Clifford Dobell, F.R.S., for kindly reading this manuscript.

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